MECHANISMS UNDERLYING PLANT COMMUNITY PRODUCTIVITY, STABILITY AND ASSEMBLY

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I dedicate this thesis to my grandfather Francesco,
who first showed me the beauty of Nature.

CONTENTS

SUMMARY

The loss of biodiversity has been a focal point for debate and interest in ecology for several decades. In particular, biodiversity loss has been extensively demonstrated to be connected with the decline of several ecosystem variables, such as reduced primary productivity and increased variability in both the productivity and the community structure of ecological communities and increased susceptibility to species invasion. However, the mechanisms that link biodiversity loss to the performance of an ecosystem remain largely unexplored and often debated. In this thesis, I use data that have been collected over a decade from a large grassland biodiversity experiment – the Jena Experiment in Germany – to identify the mechanisms through which biodiversity loss affects multiple aspects of ecosystem functioning.

In **chapter one,** I assess the temporal stability in the aboveground biomass of experimental plant communities over a period of ten years (2003–2012). I identified the relative effects of species richness, temporal species fluctuations, environmental fluctuations, community structure and functional diversity as the drivers of stability in plant community productivity. I found that asynchronous temporal fluctuations of species stabilized community productivity of the more species-rich communities. Furthermore, community structure and functional diversity both acted directly on community stability and indirectly on the asynchronous fluctuations of species to stabilize community productivity. Species richness, community structure and functional diversity appeared to partially compensate each other across time to stabilize plant community performance; environmental fluctuation instead had only small effects on community stability, thus suggesting that biotic factors, compared to the abiotic ones, are largely responsible for the stabilization of aboveground productivity.

In **chapter two,** I quantified the role of interspecific species competition in shaping community structure using Lotka-Volterra (LV) models to predict species coexistence in multispecies communities. In a glasshouse, I established a pairwise competition experiment

where all possible 2-species combinations and monocultures of 60 grassland species were planted in pots. From this experiment I derived LV parameters (growth rates, carrying capacities and competition coefficients) to run deterministic LV simulations in continuous time. These simulated results based on the pairwise competition experiment were compared with empirical field data collected over 10 years in the Jena Experiment. I found that LV predictions of plant community productivity and composition based on the glasshouse experiment were comparable to the empirical plant community data from the earlier years of the Jena Experiment. Thus, the comparison between predicted performances of the communities and the observed performances from empirical data suggest that pairwise interspecific competition holds a crucial role in the establishment of grassland communities.

In **chapter three,** I investigated the mechanisms behind species assembly by comparing artificially assembled communities and communities undergoing processes of natural reassembly within the Jena Experiment. I observed that communities undergoing natural reassembly converged in terms of species richness, aboveground productivity and community compositions regardless of the initial sown species richness of the communities. Additionally, I showed that the changes from artificially to naturally assembled communities led to reduced interspecific competition. Thus, these findings suggest that community reassembly does not depend on community history of the sown species and instead mechanisms of complementarity among species lead to convergence of community composition.

Overall, this thesis shows the complex nature of the mechanisms connecting biodiversity loss and ecosystem functioning. Specifically, plant species diversity has a clear and important role in defining community productivity and stability in productivity over many years. Furthermore, mechanisms that reduce interspecific competition likely drive species complementarity and overall community productivity and stability during plant community assembly.

ZUSAMMENFASSUNG

Der Verlust von Biodiversität ist seit Jahrzehnten im Mittelpunkt des Interessens von Ökologen und steht ebenso lange unter Debatte. Insbesondere wurde umfassend gezeigt, dass der Verlust der Biodiversität mit dem Rückgang von verschiedenen Ökosystemeigenschaften zusammenhängt, zum Beispiel mit reduzierter Primärproduktion und höherer Variabilität in Produktivität und Struktur von ökologischen Gemeinschaften, sowie auch mit einer höheren Empfindlichkeit gegenüber invasiven Arten. Allerdings sind die Mechanismen, welche den Biodiversitätsverlust mit dem Verhalten eines Ökosystems verknüpfen, noch weitgehend unerforscht, und sie werden kontrovers diskutiert. In der vorliegenden Arbeit verwende ich Daten, die über ein Jahrzehnt in einem grossen Wiesen-Biodiversitätsexperiment erhoben wurden, um die Mechanismen, welche für den Einfluss von Biodiversitätsverlust auf mehrere Aspekte von Ökosystemfunktionen verantwortlich sind, zu identifizieren.

Im **ersten Kapitel** beurteile ich die zeitliche Stabilität in oberirdischer Biomasse von experimentellen Pflanzengemeinschaften über eine Periode von 10 Jahren (2003–2012). Ich habe die relativen Einwirkungen von Artenreichtum, zeitlicher Artenfluktuation, Umweltfluktuation, Gemeinschaftsstruktur und funktioneller Diversität als Treiber der Stabilität von Pflanzengemeinschaftsproduktivität identifiziert. Ich habe herausgefunden, dass asynchrone zeitliche Artenfluktuationen die Produktivität der vielfältigeren Gemeinschaften stabilisieren. Ausserdem wirken die Gemeinschaftsstruktur und die funktionelle Diversität sowohl beide direkt auf die Stabilität der Gemeinschaft, wie auch indirekt auf die asynchronen Artenfluktuationen, um die Gemeinschaftsproduktivität zu stabilisieren. Artenreichtum, Gemeinschaftsstruktur und funktionelle Diversität scheinen sich dabei teilweise im Laufe der Zeit zu kompensieren, um so die Produktivität der Pflanzengemeinschaft zu stabilisieren. Die Umweltfluktuationen, hingegen, hatten nur kleine Einwirkungen auf die Gemeinschaftsstabilität, was darauf hindeutet, dass biotische Faktoren, im Vergleich zu abiotischen, grösstenteils für die Stabilität von oberirdischer Produktivität verantwortlich sind.

Im **zweiten Kapitel** habe ich die Rolle von zwischenartlicher Konkurrenz auf die Gestaltung der Artengemeinschaften quantifiziert, indem ich Lotka-Volterra (LV)-Modelle angewandt habe, um Artenkoexistenz in Gemeinschaften mit mehreren Arten vorauszusagen. In einem Gewächshaus habe ich ein paarweises Konkurrenzexperiment aufgesetzt, indem ich alle möglichen 2-Arten-Kombinationen und Monokulturen von 60 Wiesenarten in Töpfe pflanzte. Von diesem Experiment habe ich LV-Parameter abgeleitet (Wachstumsraten, maximale Biomassen und Konkurrenzkoeffizienten), um deterministische und zeitkontinuierliche LV-Simulationen berechnen zu lassen. Die simulierten Resultate, basierend auf dem Gewächshausversuch, habe ich mit empirischen Feldversuchsdaten, welche über 10 Jahre im Jena Experiment gesammelt wurden, verglichen. Ich konnte zeigen, dass LV-Voraussagen mit den empirischen Daten der Pflanzengemeinschaft von früheren Jahren des Jena Experiments gut vergleichbar sind. Der Vergleich zwischen der vorausgesagten Pflanzengemeinschaftsleistung und der beobachteten zeitlichen Entwicklung weist darauf hin, dass die paarweise zwischenartliche Konkurrenz bei der Etablierung von Wiesengemeinschaften eine auschlaggebende Rolle spielt.

Im **dritten Kapitel** habe ich die Mechanismen, welche der Artenzusammensetzung zugrunde liegen, untersucht. Ich habe dabei künstlich zusammengestellte Gemeinschaften mit solchen, welche im Jena Experiment nach Aufgabe des Jätens durch natürliche Einwanderungsprozesse entstanden sind, verglichen. Ich habe beobachtet, dass Gemeinschaften, welche natürlich zusammengesetzt sind, sich in Bezug auf Artenreichtum, oberirdischer Produktivität und Gemeinschaftszusammensetzung annähern, ungeachtet der ursprünglich gesäten Vielfalt der Gemeinschaft. Zusätzlich konnte ich zeigen, dass die Änderung von künstlich zu natürlich zusammengesetzten Gemeinschaften zu einer reduzierten zwischenartlichen Konkurrenz geführt hat. Diese Ergebnisse deuten darauf hin, dass die Gemeinschaftszusammensetzung nicht von der vorhergehenden

Pflanzengemeinschaft abhängig ist, sondern stattdessen Mechanismen der Komplementarität zwischen Arten zu der Annäherung von Gemeinschaftszusammensetzungen führten.

Insgesamt zeigt diese Arbeit die Komplexität der Mechanismen welche dem Verlust von Biodiversität und Ökosystemfunktionen zugrunde liegen. Insbesondere der Artenreichtum spielt eine wichtige Rolle für die Bestimmung von Gemeinschaftsproduktivität und deren Stabilität über viele Jahre. Ausserdem sind es sehr wahrscheinlich zwischenartliche Konkurrenz reduzierende Mechanismen, welche die Artenkomplementarität und die gesamte Gemeinschaftsproduktivität und –stabilität während der Entwicklung von Pflanzengemeinschaften antreiben.

SOMMARIO

Negli ultimi decenni la comunità scientifica si è concentrata sullo studio delle conseguenze della perdita di biodiversità ed, in particolare, di come questa perdita influenzi il funzionamento degli ecosistemi naturali. Diversi studi hanno già comprovato come la riduzione del numero di specie presenti in un ecosistema provochi un malfunzionamento dell'ecosistema stesso. Ad esempio, è stato ampiamente dimostrato che la perdita di specie in una comunità comporta un decremento della biomassa prodotta della comunità stessa, una maggiore fluttuazione della produttività ed una maggiore vulnerabilità all'invasione da parte di specie non appartenenti alla comunità stessa. Nonostante la ricerca scientifica abbia permesso di chiarire numerosi aspetti relativi alle conseguenze della perdita di biodiversità, non è stato ancora inequivocabilmente chiarito perchè la perdita di biodiversità causi un malfunzionamento dell'ecosistema. Questa tesi fa uso di dati raccolti durante dieci anni di studi condotti nell'ambito dello "Jena Experiment", in Germania. Nello Jena Experiment viene simulata la perdita di biodiversità in ecosistemi prativi con lo scopo di investigare i meccanismi che regolano la relazione tra il numero di specie ed il funzionamento dell'ecosistema. Questa tesi costituisce un valido contributo alla letteratura scientifica dedicata allo studio dei meccanismi inerenti l'effetto della perdita di biodiversità sul funzionamento degli ecosistemi naturali.

Nel **primo capitolo** sono stati quantificati sia la stabilità temporale della produttività delle comunità prative durante un periodo di dieci anni (2003–2012) che cinque fattori che potenzialmente influenzano la stabilità della produttività stessa. In particolare, i fattori identificati sono: numero di specie presenti nella comunità, fluttuazione temporale della produttività delle singole specie, fluttuazioni meteo-climatiche, struttura delle comunità e diversità funzionale. I risultati ottenuti mostrano come le asincrone fluttuazioni della produttività delle singole specie, compensandosi tra di loro nel tempo, causino una maggiore stabilità della produttività in comunità con piú specie rispetto a comunitá con meno specie. Inoltre, nelle comunità composte da piú specie, la struttura e la diversità funzionale

promuovono sia direttamente che indirettamente (mediando le fluttuazioni delle specie) una maggiore stabilità della produttività. Gli effetti del numero di specie, della struttura della comunitá e della diversità funzionale si compensano, almeno parzialmente, tra di loro, garantendo una maggiore stabilità temporale per le comunità piú ricche di specie. Invece, le fluttuazioni ambientali influenzano solo limitatamente la stabilità della produttività delle comunità. Si evince quindi che fattori biotici possono avere un ruolo piú importante rispetto a fattori abiotici per la regolazione del funzionamento degli ecosistemi.

Nel **secondo capitolo**, utilizzando un set di equazioni Lotka-Volterra (LV) di tipo deterministico e continuo, è stato quantificato il ruolo delle competizioni interspecifiche nel definire la struttura delle comunità. In altre parole, le equazioni LV sono state utilizzate per predire quali e quante specie possano coesistere all'interno di una comunità prativa. Per derivare i parametri necessari per le equazioni LV sono state assemblate, per le 60 specie utilizzate nello Jena Experiment, tutte le possibili combinazioni di due specie e di una specie, per un totale di 1770 vasi. Successivamente, le caratteristiche delle comunità osservate a Jena durante un periodo di dieci anni sono state confrontate con le caratteristiche delle comunità predette dalle equazioni LV. I risultati cosí ottenuti evidenziano come le predizioni e le osservazioni siano simili tra di loro nei primi anni dell'esperimento a Jena. Questi risultati suggeriscono che la competizione interspecifica svolge un ruolo importante durante la costituzione di una comunità.

Nel **terzo capitolo** si discutono i processi attraverso i quali si formano le comunità. Per questo studio sono state confrontate due tipologie di comunità prative: comunità nelle quali il numero di specie presenti è mantenuto costante artificialmente durante tutto il tempo dell'esperimento e comunità nelle quali, dopo sette anni di mantenimento artificiale, il numero di specie viene lasciato ad un regolamento mediato solo da processi naturali. I risultati ottenuti evidenziano come i processi naturali diano origine a comunità caratterizzate da simili livelli di produttività, numero e composizione di specie, indipendentemente dal

numero di specie presenti all'inizio dell'esperimento. Inoltre, è stato dimostrato come il passaggio dal mantenimento artificiale del numero di specie a quello naturale, porti ad una riduzione della competizione interspecifica. Ció suggerisce che i processi inerenti alla formazione delle comunità non dipendono tanto dalle specie presenti inizialmente nell'ambiente ma piuttosto dalla presenza di meccanismi che favoriscono un uso complementare delle risorse tra specie.

In conclusione, questa tesi evidenzia la natura complessa dei meccanismi che regolano i fenomeni ecologici e pone particolare attenzione su come la perdita di biodiversitá influenzi la funzionalitá degli ecosistemi. Difatti, il numero di specie presenti nella comunità ha un ruolo chiave nel garantire maggiore produttività e stabilità della produttività nel tempo. Infine, i meccanismi che riducono il ruolo della competizione interspecifica sono quelli che permettono un uso complementare delle risorse da parte delle specie e che quindi promuovono maggiore produttività e stabilità delle comunità.

GENERAL INTRODUCTION

Biodiversity loss and ecosystem functioning

It is now well established that our planet is facing what the scientific community refers to as the sixth mass extinction (Totten et al. 2003; Wake and Vredenburg 2008). Therefore, in the last 25 years the scientific community took increasing interest in understanding the causes and consequences of biodiversity loss, and in particular, the effects of biodiversity loss on the functioning of ecosystems. To date, a number of great advancements have been achieved and it is now generally accepted that a loss of biodiversity leads to a loss in multiple ecosystem functions such as primary productivity (Reich et al. 2012) and temporal stability of primary productivity (Lehman and Tilman 2000; Tilman et al. 2006). However, while over the years the scientific research has led to some consensus on the role of biodiversity in driving community productivity, new questions have been raised. New challenges in the study of the biodiversity–ecosystem functioning relationships aim to solve more mechanistic questions, such as how biodiversity affects the stability of ecosystem functions and how biodiversity itself is maintained, i.e. how different species can coexist. Both mechanisms of stabilization of ecosystem functions with increased diversity and mechanisms of plant community assembly and species coexistence are still unclear and debated (e.g. Pfisterer et al. 2004; Loreau and de Mazancourt 2013). Biodiversity experiments have been largely used as a tool to study the nature of the links between biodiversity, community- and ecosystem-level processes and abiotic environment (Schmid et al. 2002).

The first biodiversity experiment dates as far back as Darwin's work (Darwin and Wallace 1858), but it is only in the last few decades that the full potential of biodiversity experiments was realized. Biodiversity experiments, where the composition of species is predetermined through experimental manipulation, have been powerful tools to study both the effects of biodiversity loss on ecosystems properties and the mechanisms that regulate them (Schmid et al. 2002). In biodiversity experiments, the manipulation of the composition

of plant species and the number of species within a community, more frequently referred to as species richness or diversity, has been achieved by either removing species from a naturally assembled plant community or by assembling plant communities in a predetermined manner. History has demonstrated that grassland biodiversity experiments represent a useful model system that can help explain the role of biodiversity in natural ecosystems. Examples of these experiments are the Cedar Creek experiment in Minnesota, US (e.g. Tilman et al. 1996), the BIODEPTH study carried out across Europe (e.g. Hector et al. 1999), the Ecotron in the UK (e.g. Naeem et al. 1994) and the Jena Experiment, in Germany (e.g. Roscher et al. 2004; Allan et al. 2013). The Jena Experiment is one of the longest lasting and most intensively measured experiments (Allan et al. 2013). Established in 2002 and still ongoing, the Jena Experiment has been used for more than 1500 documented field-activities and measurements to understand the role of biodiversity for the functioning of ecosystems (www.the-jena-experiment.de).

The Jena Experiment has already largely contributed to expand the current understanding of biodiversity–ecosystem functioning mechanisms in a broad range of sectors. Different studies investigated the mechanisms behind i) the biodiversity–element cycles relationship, also in multitrophic studies (e.g. Roscher et al. 2004; Scherber et al. 2010; Eisenhauer et al. 2012), ii) the biodiversity–productivity relationship (e.g. Marquard et al. 2009), iii) the biodiversity–stability relationship (e.g. Roscher et al. 2011) and iv) the biodiversity–soil carbon storage relationship (e.g. Steinbeiss et al. 2008). Well established long-term biodiversity experiments have not only been a basis for our current knowledge on how more diverse plant communities function, but have also opened doors for further hypotheses with regards to the temporal functioning of communities and the mechanisms by which species may coexist and natural communities are assembled.

Mechanisms underlying temporal stability of community productivity

In the context of climate change, it is crucial to understand how biodiversity loss will affect long-term ecosystem functioning. Thus, the question we need to answer is if and why species-rich ecosystems are more stable in their functions over time. Understanding the drivers of the stability of ecosystem functioning is not only a mere academic question but it is especially crucial in the context of a world undergoing severe climate change. Climate change is not anymore considered as a remote threat, as the effects are unequivocally visible (Solomon 2007). These changes have potentially large impacts on the stability and the functioning of natural ecosystems via the modification of the abiotic environment or through indirect effects on species composition and richness (Crutzen 2002). Understanding what makes some communities more stable across time than others is therefore of great help in predicting, and hopefully reducing, the negative effects of biodiversity loss.

Plant productivity and temporal stability of productivity have been extensively used as a proxy of ecosystem functioning in the study of the effects of biodiversity loss (Tilman et al. 1996, 2006; Hector et al. 1999; Cardinale et al. 2004; Roscher et al. 2004; Balvanera et al. 2006). However, which mechanisms mediate the positive effect of species richness on temporal stability of community productivity has not yet been fully clarified. A great majority of biodiversity experiments have shown that more diverse communities are more productive and more stable in their productivity over time. This effect of greater species diversity in stabilizing the community performance has been explained through an insurance effect of biodiversity (Bai et al. 2004; Ives and Carpenter 2007). The insurance effect is an inherent result of greater species richness or biodiversity where increasing the level of species diversity by including more species simultaneously increases the likelihood that species differ in their competitive ability and in niche requirements. Classic theoretical work, however, would lead to the opposite conclusions, suggesting that an increase in species

richness, and therefore complexity of the communities is accompanied by a decrease of stability at the species level due to increasing competition (May 1973).

In order to clarify this debate, different authors suggested various methods to quantify the drivers behind community stability. The previous attempts to disentangle the mechanisms trough which more species-rich communities ensure higher temporal stability of community productivity were formulated by Tilman et al. (2006), Loreau and de Mazancourt (2008) and Loreau and de Mazancourt (2013). In this general introduction I will not explain in detail the characteristic of these methods as I largely discuss them in chapter 1. In summary, these authors attempted to quantify the mechanisms behind the increased stability of species-rich communities from measures of i) overyielding, ii) temporal inter- and intraspecific interactions, iii) species responses to environmental fluctuations and iv) stochastic demographic fluctuations. However, it is generally agreed that these mechanisms are likely to interplay with each other across time (Loreau and de Mazancourt 2013) so that their quantification and the application of the theoretical framework to more natural conditions has been so far unsatisfactory (but see de Mazancourt et al. 2013). A new approach, capable of measuring relative importance of different drivers across time, is therefore necessary to improve our understanding of how species-rich communities sustain larger productivity.

Species coexistence

Understanding how biodiversity loss affects ecosystem functioning requires answering first another question: how biodiversity per se exists, or namely, how different species coexist in a community. The scientific community has long been studying the processes that determine the number of species and the species composition of plant communities in order to predict multi-species coexistence. The understanding of how communities assemble (further discussed in the section *Community assembly*) is the general framework in which we operate

when looking at processes leading to species coexistence (Hille Ris Lambers et al. 2012 fig. 1).

Although there is still a lively debate regarding the mechanisms of species coexistence, it is generally accepted that species coexistence derives from an ensemble of abiotic and biotic factors operating simultaneously in different spatiotemporal scales (Hille Ris Lambers et al. 2012). For example, on a local scale environmental effects are thought to be responsible for the selection of the species that could potentially enter a community from a larger regional pool (environmental filtering, Kraft et al. 2014). Biotic processes instead are identified on a smaller spatial scale, where processes of species interaction increase of their importance (Chesson 2000; Hille Ris Lambers et al. 2012; Kraft et al. 2014). The disentangling of biotic and abiotic mechanisms is challenging (Hille Ris Lambers et al. 2012; Kraft et al. 2014), because these mechanisms are likely to operate simultaneously. In chapter 2 of this thesis I will focus on the role of the biotic effects in defining species coexistence. This does not mean in any way to suggest that abiotic factors should not be considered; instead I aim to present a restricted portion of the largest picture of community assembly, the picture of "coexistence theory".

A good overview of the potential biotic mechanisms and theories of species coexistence was provided by Chesson (2000), and is still well accepted (Cardinale et al. 2009; Hille Ris Lambers et al. 2012). Chesson (2000) showed that for a large number of models and systems, species coexistence derives from a balance of equalizing and stabilizing mechanisms. Equalizing mechanisms, lately redefined as relative fitness differences (Hille Ris Lambers et al. 2012), reduce fitness differences among species so that the effect of interspecific interactions on population dynamics is reduced. Equalizing mechanisms are those differences between species that predict the outcome of competition in the absence of stabilizing mechanisms. The extreme case of an equalizing mechanism fits within the framework of a neutral theory of biodiversity (Hubbell 2001; Bell 2001). According to

Hubbell (2001), if demographic parameters are identical across species, species dynamics and therefore coexistence depend solely on stochastic events (Chesson 2000; Hubbell 2001; Bell 2001; Adler et al. 2007). However, equalizing mechanisms are ecologically unlikely. Thus, to allow long-term coexistence some sort of stabilizing mechanisms need to be operating as well.

Stabilizing mechanisms are identified as any type of temporal or spatial niche differentiation (Chesson 2000; Cardinale et al. 2009). Stabilization through niche differentiation, regardless of whether it occurs through partitioning of limited resources, temporal differentiation of resource requirements or predator pressure, or some other dimension of niche space, always reduces competition among species relative to competition within species (i.e. negative frequency dependency, Chesson 2000; Levine and Hille Ris Lambers 2009). The quantification of competition among species (interspecific competition) and within the same species (intraspecific competition) is therefore crucial to predict species coexistence.

Stabilizing and equalizing mechanisms are not mutually exclusive in driving species coexistence. Therefore, it is necessary to identify the role of each of them along spatial and temporal scales (Cardinale et al. 2004). At larger scales, the relative importance of indirect interspecific competition (the effect that a species might have on the interaction among other species) is predicted to increase because the role of indirect mechanisms increases with the increasing number of species considered, or in other situations with the spatial scale considered (Dormann and Roxburgh 2005; Weigelt et al. 2007). Furthermore, both interspecific competition and stochastic events might change in importance along the temporal scales that apply to natural systems (Cardinale et al. 2004).

Pairwise competition experiments are a useful tool to quantify the direct role of each species on its neighbors (Connolly et al. 2001; Connolly and Wayne 2005; Weigelt et al. 2007) and to disentangle it from the indirect effects of one species on the interaction among

other species (Wootton 1994a; b; Weigelt et al. 2007; Engel and Weltzin 2008). The use of Lotka-Volterra models is one of the most common way to analyze pairwise competition experiments and thus to derive the role of direct interspecific competition (Grover 1997; Chesson 2000; Dormann and Roxburgh 2005).

Community assembly

In the search of the mechanisms behind biodiversity–ecosystem functioning relationships the scientific community has more recently started to consider how communities assemble, namely how species enter a community and how their abundances changes over time (Fukami and Morin 2003). Classically, the mechanisms of community assembly have been divided into deterministic and historically contingent approaches (Fukami et al. 2005). The deterministic approach and the historically contingent approach can be related, respectively, to the concepts of niche theory and of neutral theory (see section *Species coexistence*).

The deterministic approach suggests that communities converge towards a common structure determined by the environmental conditions and by the available niche space in the communities (Clements 1916; Elton 1958; Fukami et al. 2005; Adler et al. 2007; Petermann et al. 2010). Thus, intra- and interspecific species competition would define species coexistence. This, however, has been hotly debated because in some cases species coexistence could be explained without the use of niche theory or other biotic processes (Connor and Simberloff 1979; Hubbell and Foster 1986; Hubbell 2001). Instead, the neutral theory of biodiversity suggests that community assembly is historically contingent so that the sequence of species arrival in the community can cause divergence in community structure even under identical environmental conditions and with species pools (MacArthur and Wilson 1967; Hubbell 2001; Fukami and Morin 2003; Fukami et al. 2005).

To solve this debate, it has been suggested that the convergence or divergence of community composition is related to the community organization considered (Wilson 1999;

Fukami et al. 2005). The functional groups present in the community are thought to be determined on the basis of the trait-space supported by that specific environment while the species that will constitute the community are instead thought to be randomly derived (i.e. historically contingent) within each trait-based group (Fukami et al. 2005). Previous experiments have validated this formulation: for example, Fukami et al. (2005) showed that environmental conditions defined the available niche space (i.e. via environmental filtering, see section: *Species coexistence*). Species selection within each trait-based group was instead random, supporting the historically contingent approach.

The niche theory suggests that species entering the community organize in order to maximize the utilization of the biotope space (Chesson 2000). Thus, niche differentiation and consequentially reduced interspecific competition lead to an increase of the complementarity effect in the communities (Loreau and Hector 2001; Levine and Hille Ris Lambers 2009). Increased complementarity has been advocated as the factor responsible for the improvement of ecosystem functions in more diverse communities over time (Hille Ris Lambers et al. 2004; Tilman et al. 2006; de Mazancourt et al. 2013; Zuppinger-Dingley et al. 2014). However, larger species richness also corresponds to larger probability to include a species in the community that contributes un-proportionally to the ecosystem functioning, a process known as selection effect (Loreau and Hector 2001). In some cases the selection effect can explain a positive biodiversity effect on ecosystem functioning (e.g. Wagg et al. 2011). Therefore, the quantification of complementarity and selection effects in invasion experiments used to study community assembly (Pfisterer et al. 2004; Fukami et al. 2005; Bezemer and van der Putten 2007; Rixen et al. 2008) would indicate if mechanisms of species complementarity or of species dominance drive community assembly in these experiments.

Different studies have previously shown how the species that provide a given function in a specific period of time might differ from the species providing the same function across a

longer time period (Yachi and Loreau 1999; Tilman et al. 2006; Zavaleta et al. 2010; Isbell et al. 2011). Thus, the temporal scale considered and the measurement of mechanisms and ecosystem functions over longer time periods are also of crucial importance because different species and different mechanisms might promote different ecosystem functions in different years.

Thesis outline

This thesis focuses on the mechanisms behind the biodiversity–ecosystem functioning relationship. I investigated both the effects of biodiversity loss on ecosystem functioning and the mechanisms driving the ecosystem changes as a consequence of biodiversity loss. First, I investigated the effects of biodiversity loss on temporal stability of productivity and I identified the drivers responsible of the stabilization of more diverse communities (chapter 1). Next, I investigated the mechanisms of species coexistence, focusing in particular on the role of interspecific competition (chapter 2). Finally, I used the transition from artificially to naturally assembled communities to study the mechanisms and consequences of community assembly (chapter 3).

In **chapter 1,** I discuss the mechanisms behind the increased temporal stability of productivity in more diverse communities. The effects of asynchronous fluctuation of species biomass, of community evenness, of community functional trait distance and of environmental fluctuations on temporal stability of community biomass are analyzed over a period of 10 years.

In **chapter 2,** I investigate the mechanisms behind species coexistence. Specifically, I used Lotka-Volterra models to predict multi-species performances on the basis of a pairwise competition experiment carried out in a glasshouse. The Lotka-Volterra predictions of community performances were then compared to 10 years of observed community

performances in the Jena Experiment in order to evaluate the role of interspecific species competition in defining species coexistence.

In **chapter 3,** I explore the mechanisms of community assembly. I used artificially assembled communities where a weeding treatment maintained the original sown species richness and I compared them to portions of these communities were the weeding treatment was stopped. The comparison between the performances of these two community types allowed us to further our understanding about mechanisms of community assembly.

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CHAPTER 1

Asynchronous species fluctuations are the main driver of community stability in experimental plant communities

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Abstract

A predominant effect of biodiversity on ecosystems is the temporal stability of species-rich plant communities. However, which biotic and abiotic factors are responsible for the increased stability of more diverse communities, is still an open question.

In this study we used species specific aboveground biomass measured for a 10-year period in the Jena Experiment, Germany, to investigate temporal patterns of community stability. We first calculated community stability and identified five potential drivers of it: species richness, temporal species fluctuations, environmental fluctuations, community structure and functional diversity. We then used general linear and structural equation modelling to quantify the contributions of these drivers and their interactions.to community stability.

Our results showed that asynchronous temporal fluctuations of species populations were mainly responsible for the increased stability of more species-rich communities. Furthermore, community structure and functional diversity both acted directly on community stability and indirectly via the asynchronous species fluctuations. Environmental fluctuations had little effects on community stability. Finally, different drivers affected community stability at different time intervals, partly compensating each other influence. These results are congruent with postulates of an insurance effect of diversity and with niche theory. They support the hypothesis that compensatory dynamics originating at the species level are able to stabilize aboveground biomass production at the community level.

Keywords: biodiversity loss, community stability, evenness, functional trait diversity, environmental variation, synchrony

Introduction

Biodiversity loss, such as the decline in species richness, has repeatedly been shown to negatively affect plant productivity (Tilman et al. 1996; Hector et al. 1999; Roscher et al. 2004). Moreover, a greater richness of species can be instrumental in maintaining a consistent level of ecosystem performance across environmental changes through time (MacArthur 1955; McNaughton 1977; Lehman and Tilman 2000; Flynn et al. 2008; Proulx et al. 2010; Isbell et al. 2011; Hautier et al. 2014). Higher levels of biodiversity can have a positive effect on various community properties that may contribute to the overall stabilization of community performance. For instance, greater species richness positively affects the capability of a community to recover from abiotic perturbations, such as drought (Mulder et al. 2001; Van Ruijven and Berendse 2010) and resist biotic perturbations, such as species invasion (Hector et al. 2001). The speed with which the ecosystem recovers after perturbations (resilience) and the degree to which it recovers (resistance), can also be increased by greater species richness (Griffiths et al. 2000; Mulder et al. 2001). These increased community responses to environmental perturbation are thought to be due to a greater insurance that some species will be able to provide to community stability (Yachi and Loreau 1999). However, greater community stability in more species-rich communities may not always be associated with greater resistance and resilience (e.g. Tilman and Downing 1994; Tilman 1996; Pfisterer and Schmid 2002; Van Ruijven and Berendse 2010; Vogel et al. 2012). Thus, the mechanisms underlying the effects of greater species richness on community stability in experimental studies and natural ecosystems may be a result of multiple driving factors and remains hotly debated (de Mazancourt et al. 2013).

Positive effects of species richness on community stability (CS) have been frequently shown, both empirically and theoretically, to correlate with increasing temporal oscillations at the level of species populations (Flynn et al. 2008; Loreau and de Mazancourt 2008, 2013; Isbell et al. 2009). This is known as portfolio or insurance effect (Bai et al. 2004; Ives and

Carpenter 2007). The effect may arise from the increased likelihood that species that co-occur in species-rich communities differ in their phenology, resource requirements and tolerance to environmental perturbations. Moreover, temporal niche differentiation allows for compensatory dynamics of co-occurring species in response to abiotic changes (i.e. asynchronous fluctuations), therefore maintaining community performance throughout time. Some theoretical work, however, suggest that in some cases biodiversity can decrease rather than increase community stability. As species richness increases, so does complexity of the communities, and competition in such complex systems might in fact decrease the stability at least at the species level (May 1973) if not at the community level (Tilman 1999). While this notion of biodiversity begetting instability had been relatively dormant for the last two decades, a recent simulation study by Loreau and de Mazancourt (2013) has rekindled interest in this idea.

Elucidating this debate requires an examination of the mechanisms underlying the relationship between biodiversity and stability. Traditionally, the main drivers considered have been overyielding, species covariance and statistical averaging (Tilman et al. 2006). Overyielding refers to a situation where more diverse communities produce more biomass and thus competitive interactions are relaxed. Negative covariances between species can result from competitive interactions or from contrasting species responses to environmental variation. Finally, statistical averaging results from the scaling of species abundances with increasing species richness. Of these three, species covariances have been used extensively as a mechanistic explanation for biodiversity−stability relationships, but there are mathematical and logical constraints in how easily this can be tested (Loreau and de Mazancourt 2008, 2013). First, the sum of negative covariances among species abundances does not allow for a distinction between the different potential causes of asynchronous species fluctuations. Second, with this metric it is not possible to separate the contributions of the individual temporal covariances between the different species pairs to the community-level behavior

(Brown et al. 2004; Loreau and de Mazancourt 2008).

A second approach to identifying the mechanisms behind the biodiversity−stability relationship models the population dynamics of the different species in a community in response to a fluctuating environment, which then can predict levels of species asynchrony in the presence or absence of species interactions (Loreau and de Mazancourt 2008). In this framework, there are three alternative drivers of community stability: i) intra- and interspecific density dependence, the latter occurring in the presence of species interactions, ii) environmental stochasticity, which quantifies the different species responses to environmental fluctuations in the absence of species interactions and iii) demographic stochasticity that results from different population structures of the species in the community, again in the absence of species interactions. This model has been applied empirically in part (de Mazancourt et al. 2013), but its application to field-collected data has several limitations. First, the model can only be used as a null hypothesis to test the effect of species differences on species asynchrony. Additionally, in grasslands, which often serve as model ecosystems for biodiversity−stability studies, information about the demography of different species is not easily quantified, with substantial challenges in monitoring perennial and clonal herbaceous species. More recently, Loreau and de Mazancourt (2013) proposed an alternative theoretical framework for biodiversity−stability relationships, based on temporal complementarity (asynchronous degree and speed of responses to environmental fluctuations) and functional complementarity. However, the relative importance of all these potential driving factors of community stability has yet to be quantified in detail with experimental field data to provide a better understanding of the role that biodiversity may play in sustaining ecosystems.

Here we develop an approach applicable to field data to disentangle components of the biodiversity−stability relationship. Specifically, we aim to identify the drivers behind the stabilizing effect of more diverse communities by assessing the relationships among multiple

drivers. We use data from a long-term grassland biodiversity study, the Jena Experiment (Roscher et al. 2004; http://www.the-jena-experiment.de/), with ten years of experimental field data on plant performance at the community and species level, as well as data about species traits and environmental characteristics. Using these data we calculate plant community stability (μ/σ) and five of its potential drivers: species richness, temporal species fluctuations, environmental fluctuations, plant community structure and plant functional trait diversity. We test the following six hypothesis of increasing complexity, depicted in Fig. 1, by progressively adding the identified drivers to the explanatory model: 1) species richness drives community stability, 2) this happens via asynchronous species fluctuations, 3) species fluctuations are driven by environmental fluctuations, 4) community structure defines how species fluctuate in response to the environmental fluctuations, 5) plant functional trait diversity or 6) plant functional trait diversity and community structure are responsible for how species fluctuate in response to environmental fluctuations. We used structural equation modeling (SEM) to assess both the direct and indirect contributions of these drivers, starting from the paths evidenced by the winning hypothesis. The hierarchical structure of the direct and indirect effects of the driving factors of community stability are depicted in Fig. 2.

Materials and Methods

The analyses were carried out using data from the Jena Experiment, a large biodiversity experiment established in mesophilic mown central European grassland (Roscher et al. 2004). The experiment started in 2002 with a pool of 60 grassland species, which were used to assemble communities of sown species richness 1, 2, 4, 8, 16 and 60 species on a total of 82 plots (see Roscher et al. 2004 for field site and design specifics).

Aboveground biomass was harvested twice per year, once in spring (late May – early June) and once in summer (late August – early September). Plants were harvested by cutting randomly selected subplots of 0.2 x 0.5 m at 3 cm above ground level. A different number of

subplots were harvested in the different years: four subplots in years 2003–2007, three subplots in years 2008–2009 and two subplots in years 2010–2012. Plant material was sorted to species, dried at 70 C° for 48 h and weighed. Aboveground species biomass per harvest was calculated as the average of the subplot samples per plot. For further details, see Weigelt et al. (2010). For our study we used the peak biomass data (spring harvest) collected from 2003–2012.

Indices of community and environmental characteristics

We identified the following five drivers of community stability and for each driver we calculated one or more indices. For each driver, we then selected the index with the highest explanatory power as the representative index for the given driver.

Community stability — We calculated community stability (*CS*) as the inverse of the coefficient of variation in community aboveground biomass (Lehman and Tilman 2000) for each 1-year time interval, e.g. between 2003 and 2004 or between 2004 and 2005, as:

$$CS = m/sd$$

where m is the mean and sd is the standard deviation of the two years. CS was $\log_2$-transformed.

Drivers:

I Species richness — Our basic assumption was that species-rich communities should be more stable than species-poor communities. We used the number of sown species as index of species richness. Because the experimental communities were regularly weeded and only four of the sown species went extinct, this driver was closely correlated with the realized plant species richness determined by cover estimates (Marquard et al. 2009). For all

analyses species richness was $\log_2$-transformed to linearize its logarithmic relationship with productivity.

II Temporal species fluctuations — We identified three indices of temporal fluctuations in species aboveground biomass values: the sum of covariances (Hubbell 2001), the synchrony index (Loreau and de Mazancourt 2008) and the number of realized interactions (May 1973; Bai et al. 2004). Covariance (cov) is a measure of how much two random variables change together. When compensatory dynamics and common responses to abiotic changes level off, the sum of covariances

$$sum\_of\_cov = \sum cov(x_i, x_j)$$

will be 0; values below 0 indicate that compensatory dynamics are driving community dynamics, while values above 0 indicate that species respond in similar ways to environmental changes.

We additionally used the synchrony index as measure of temporal fluctuations (Loreau and de Mazancourt 2008). This index is standardized between 0 (perfect asynchrony of the species in the community) and 1 (perfect synchrony). We calculated it following the rewriting of the formula from Roscher et al. (2011):

$$sync = \frac{\sum(\sigma^2(x_i)) + \sum cov(x_i, x_j)}{(\sum \sigma^2(x_i))^2}$$

where x_i is again the biomass of species i, and $cov(x_i, x_j)$ measures covariance between two species. The synchrony index was $\log_2(sync + 0.01)$-transformed to improve homoscedasticity in the data.

Finally, we used a third index of temporal fluctuations, the sum of realized interactions (C). C was derived from the work of May (1973) and was calculated as follows

$$C = count\left(\left|\frac{\sum cov(x_i, x_j)}{\max(|\sum cov(x_i, x_j)|)}\right| > 0.5\right)$$

This index counts the number of realized interactions as the number of pairwise covariances that are stronger than 50% of the strongest covariance measured. We consider the absolute value as we did not mean to distinguish between positive and negative interactions.

III Environmental fluctuations — We assessed abiotic environmental variation over time as a potential factor affecting the stability of the community (Ives and Carpenter 2007; Loreau and de Mazancourt 2013). The data were collected from the Jena weather station located at the field site, which measured every half hour common climatic variables. We defined spring as March, April and May; summer as June, July and August; winter as December, January and February and we calculated: i) sum of rainfall in spring, ii) sum of rainfall in summer, iii) growing-degree days in spring (number of days with daily mean temperature > 5°C), iv) growing-degree days in summer, v) frost-days in winter (number of days with daily maximum temperature < 0°C), vi) vegetative days per year (number of days between the first and the last day with mean daily temperature ≥ 5°C) and vii) first day at mean daily temperature ≥ 5°C (counted from the 1st of January) (see Appendix B for further details). These summary climatic variables represented conditions over the whole experimental site; thus in any given year, the abiotic indices derived from the summary climatic variables had the same values across all plots (a description of abiotic indices is provided in Appendix B). Two combined indices of the seven abiotic indices were obtained using principal components analysis (PCA) as the first and the second principal component (*env-PC1* and *env-PC2*). The temporal variation for each consecutive year of the experiment was also calculated for the seven abiotic indices (environmental variation indices) and again two combined environmental variation indices calculated by PCA (*env-cv-PC1* and *env-cv-PC2*). In the first PCA, the first principal component (*env-PC1*) explained 30% of the variation while the second (*env-PC2*) explained 27% of the variation. In the second PCA, the

first principal component (*env-cv-PC1*) explained 33% of the variation while the second (*env-cv-PC2*) explained 24% of the variation.

IV Plant community structure — Community structure is expected to be relevant to community stability. The degree of dominance can influence stability, in particular with greater species evenness predicted and observed to relate to greater community stability (Doak et al. 1998; Cottingham et al. 2001; Roscher et al. 2011; Thibaut and Connolly 2013). Therefore, we used the evenness index (also known as equitability index) as a measure of community structural changes over time, which was calculated as

$$equit = \frac{1}{\sum {p_i}^2} \times \frac{1}{n}$$

where p_i is the proportional abundance (derived from the aboveground biomass measures) of species i, and n is the number of sown species in the community. The evenness index lies in the interval (0,1) and ranges from $1/n$ (maximum unevenness) to $\left(\sum\left(1/n\right)^2\right)/n$ (maximum evenness). As the evenness index refers to the community composition at a given time and since we are looking at time intervals, two types of indices were calculated: one considering the community composition in the first of the two years of the interval (*equit*), and one considering the average between the two years of the interval (*equit1*).

The evenness of monocultures is difficult to define conceptually. The above definition yields 1 for monoculture, that is maximum evenness. This is consistent with the results of a biodiversity × evenness experiment in Jena which showed by extrapolation that monocultures can be considered to represent maximal evenness (Schmitz et al. 2013).

V Plant functional trait diversity — Functional traits characterize morphological, physiological and phenological aspects of individual plants, which determine their growth, survival and reproductive success (Violle et al. 2007). Trait data were collected from

monocultures in late May 2006 or 2008 at the time of peak biomass (51 species in 2006, six species in 2008). For three of the species, measurements were taken in species-poor mixtures in May 2006 due to their extremely low performance in monoculture (Roscher et al. 2012, see also Appendix A for a complete description of all traits).

We used two community-wide indices of functional trait composition: community weighted means of traits values (*CWM,* e.g. Lavorel et al. 2008) and functional diversity based on the total branch length of a trait-based dendrogram (*FD*, Petchey and Gaston 2002, 2006). These two indices support two contrasting hypothesis: *CWM* quantifies the dominant trait values in a community and follows the hypothesis that ecosystem processes are mainly determined by functional traits of dominant species in the community. *CWM* was calculated from trait values weighted by species relative abundances in the community as:

$$CWM = \sum p_i t_i$$

where p_i is the relative abundance of species i and t_i is the species-specific trait value.

A standardized principle component analysis (PCA) was performed to summarize the *CWM* values for different traits in the communities. The first PCA axis accounted for 28% of the variation and the second for 23%. Trait diversity measured as *FD* tests the hypothesis that trait dissimilarity among species in the community allows for a better use of resources. We selected this index instead of other indices of traits diversity because it decreases monotonically as species are removed from a community, a feature that does not hold for example for *Rao's Q*.

It is important to note, however, that the role of functional trait composition might be underestimated due to challenges in identifying which traits are most important in driving ecosystem function. The interpretation of both *CWM* and *FD* needs to consider the selection of traits used. If the traits we measure are not able to capture the different niches exploited by the species, the measures of functional diversity are unlikely to predict community dynamics

well (Petchey and Gaston 2006).

Data analysis

Since we identified different indices for the different drivers of *CS* (see previous section), we first assessed the influence each index of each driver separately by mixed-effect models to determine which of the indices held the most explanatory power when ignoring all other indices. These mixed models included in addition to the tested index the random-effects term plot and year as factors with 82 and 9 levels, respectively. This led us to the selection of the following indices: log-transformed species richness (*div*; driver I), log-transformed synchrony index (*sync*; driver II), the second PC of temporal environmental variation (*env-cv-PC2*; driver III), the evenness index of plant community structure in the first of the two years of the interval (*equit*; driver IV) and functional diversity (*FD*; driver V). These indices were then used for further analysis in both mixed-effect general linear models and structural equation models (SEM). The general linear model approach allowed us to compare the six hypothesis we formulated in a sequential aggregation way using explanatory power and therefore to understand which drivers were responsible for community stabilization. The SEM approach allowed us to test the strength of direct and indirect effects of the various drivers of CS (Grace 2006).

The general linear models were constructed by step-wise addition of potential drivers, where each hypothesis is represented by a model. We then utilized R^2, AIC and AIC weights (relative performance of each model compared to the best one) to assess all potential models and make model selection (Table 1). Interactions between explanatory variables (the above-selected indices) were also tested, but generally did not improve the explanatory power of the models and thus were excluded from all models. For the first two models in Table 1 the only random-effects term was plot because here the average *CS* across years was tested. For the subsequent model 3–6 the random-effects term year was also included because here we tested

also variation in *CS* among years. Dependency of *CS* terms between consecutive time intervals was corrected with autocorrelation of order 1 for years.

The results of these general linear models were then used to create potentially meaningful structural equation models (SEM). A separate SEM was created for each of the nine time intervals. By performing different SEMs for each time interval we were able to assess how the percentage of variance explained by the model (R^2 associated with *CS*), the percentage of variance held by the different drivers (R^2 associated with the different drivers) and the path coefficients varied across the years. We considered the log-transformed species richness (*div*) as the only exogenous variable which potentially affected the log-transformed community stability (*CS*) via the endogenous variables functional diversity (*FD*), evenness (*equit*) and log-transformed synchrony (*sync*). The structure of the different SEMs corresponding to hypothesis 1–6 is shown in Fig. 1. Although environmental characteristics were included in the general linear models, it was not possible to include them into SEMs because each SEM referred to a specific time interval and all plots had the same value of environmental variation for a particular time interval.

All mixed-effects general linear models were carried out with GenStat (15th Edition) using the residual (=restricted) maximum likelihood method and analysis of variance (ANOVA) type of output. SEMs were calculated using Amos 21 (Amos Development Corporation, Crawfordville, Florida, USA). For the calculation of PCAs for the environmental data we used the software R, v3.0.2 (R Development Core Team, http://www.R-project.org). Additionally the CWM values were calculated using the package *FD* v11 of R (http://www.thetrophiclink.org).

Results

Effects of each driver on community stability and on species synchrony

Community stability (*CS*) increased as a function of log-transformed species richness ($F_{1,79.7}$ = 34.92, $P < 0.001$, slope = 0.23, Fig. 3a). Additionally, we observed an overall negative association between the temporal stability of individual species aboveground biomass and species richness, suggesting that compensatory dynamics of an insurance effect in more species-rich communities may have been the underlying mechanism of the increased community stability (Fig. 3b). However, the outcome of the index comparisons revealed that besides species richness other indices also contributed to the overall variation in *CS*. Specifically, we found that variation in species synchrony, community evenness, environmental variation and functional diversity also contributed to variation in *CS* (Table 2). Species synchrony had a strong negative effect on community stability ($F_{1,642.4}$ = 727.42, $P <$ 0.001, Fig. 4a). Similarly, community evenness reduced *CS* ($F_{1,731}$ = 34.71, $P < 0.001$, Fig. 4c). Conversely, environmental fluctuations and functional diversity both were positively associated with *CS* ($F_{1,7}$ = 7.49, P = 0.03, Fig. 4b and $F_{1,78.7}$ = 21.97, $P < 0.001$, Fig. 4d respectively).

Overall, species synchrony in a community (Loreau and de Mazancourt 2008), decreased with species richness (*div*, $F_{1,80.8}$ = 191.06, $P < 0.001$, R^2 = 0.24, Fig. 5a) and with functional diversity (*FD*, $F_{1,79.8}$ = 111.49, $P < 0.001$, R^2 = 0.20, Fig. 5b) and increased with increasing evenness (*equit*, $F_{1,731}$ = 139.18, $P < 0.001$, R^2 = 0.16, Fig. 5c). Environmental fluctuations, however, did not influence the variation in species synchrony (*env_cv_PC2*, $F_{1,731}$ = 0, $P > 0.98$, R^2 = 0)

Sequential model

Each model fit is given in Table 1. Adding the synchrony index increases drastically the fit of

the model (–500 AIC points and from 0.06 to 0.52 R^2 between models 1 and 2). The first two models had the lowest AIC weights. Models 4 and 6 both had the lowest AIC values and the highest explanatory power, with similar predictive ability for both (Table 1).

Structural equation modeling

The outcome of the SEM models for each time interval showed that the explanatory power held by each endogenous variable (R^2) fluctuated over time, without showing a clear temporal trend (Fig. 6). Similarly, path coefficients between *CS* and its drivers (Fig. 7, left panel) did not show any clear pattern of increase or decrease over time, except for the synchrony−stability relationship, which decreased over time. Path coefficients between species synchrony and the indices that drive it revealed evidence of compensatory influences of *equit*, *FD* and *div* (Fig. 7, right panel). Significant paths ($P < 0.05$) were those with coefficients > 0.2 or < –0.2 (Fig. 7). The paths that remained significant across the whole time spam of this study were *sync*→*CS* (Fig. 7, left panel), *FD*→*sync* and *equit*→*sync* (Fig. 7, right panel). The indices *equit*, *FD* and *div* were always negatively associated with species synchrony (only one point showed a positive non-significant path coefficient for *equit*, Fig. 7, right panel).

Correlations between R^2 and path coefficients with environmental variation did not provide evidence that environmental fluctuations contribute to the variation in the strength of the paths between the indices of temporal community characteristics ($P > 0.10$ associated with R^2; $P > 0.10$ associated with paths to *CS*).

Discussion

Several previous biodiversity experiments showed that community stability (*CS*) generally increases with species richness (Tilman 1996; Yachi and Loreau 1999; Hector et al. 2010; Roscher et al. 2011). Here we analyzed how this effect might be mediated by intermediary

variables. We identified several drivers which simultaneously influences *CS*. The drivers could be incorporated into a path model leading from species richness via community evenness, functional diversity and species synchrony to *CS* (see Fig. 2), demonstrating the complex nature of biodiversity–stability relationships. We show for the first time that the strength of the different paths from species richness to *CS* can vary between years in experimental grassland plots. Generally, *CS* increased with species richness mainly because of the negative effect of the latter on species synchrony. The cause of the negative effect of species richness on species synchrony itself seemed to be that the differential responses of the species are due to their differences in functional traits, reflected in functional diversity and in decreasing evenness of species abundances in the community, rather than to differences in species responses to environmental fluctuations over the years.

Species synchrony and community stability

Our results provide further evidence that species synchrony holds a crucial role in destabilizing plant communities. The synchrony index in fact had the highest explanatory power compared to all other drivers of *CS* (see Table 2) such that adding it to the model increased the explanatory power considerably (comparing models 1 and 2, Table 1). This was confirmed by the results of the path analysis (SEM) where the synchrony index represented the most relevant predictor of *CS* both overall and during each time interval (R^2 in Fig. 6 and path coefficients in Fig. 7). Moreover, not only did we find that species synchrony decreased *CS*, but we also found that this effect tended to increase over time.

Previous studies also highlighted that asynchronous fluctuations among plant species within a community can stabilize more diverse communities (Isbell et al. 2009; Roscher et al. 2011; Loreau and de Mazancourt 2013; Thibaut and Connolly 2013; Hautier et al. 2014). However, it appears that the scientific community is agreeing only very recently upon the measure of temporal species fluctuations to be used when investigating biodiversity–stability

relationship (Loreau and de Mazancourt 2013; Thibaut and Connolly 2013). Our results suggest that the synchrony index best captures information about changing species interactions over time. The synchrony index does not suffer from mathematical constraints which instead restrict the soundness of previous measures of species interactions such as the sum of species covariances. The synchrony index also does not make any assumptions about the particular distribution of pairwise correlation coefficients (Loreau and de Mazancourt 2008; Thibaut and Connolly 2013). Instead, there are mathematical properties of the synchrony index that relate it to the measure of *CS* (Thibaut and Connolly 2013; Hautier et al. 2014), thus indicating how the synchrony index, better than other indices, quantifies species fluctuations (Tilman and Downing 1994; Loreau and de Mazancourt 2013; Hautier et al. 2014).

In this section we showed that overall asynchronous species fluctuations can stabilize community productivity and that the measure that best explains this finding is the synchrony index (Loreau and de Mazancourt 2008). The section that follows moves on to consider how species richness, environmental fluctuations, plant community structure and plant functional trait diversity shape the biodiversity–stability relationship.

Drivers of asynchronous fluctuations of species

Our results suggest that community structure, functional diversity and species richness operate together to desynchronize species dynamics in more diverse communities. Based on the variation explained by each evenness, functional diversity or species richness individually (Table 2), or together when fitted sequentially (Table 1), we conclude that they contributed relatively equally to the stabilization of communities. It is difficult to quantify the relative importance of each of these drivers of *CS* using the general linear model approach. Structural equation modelling (SEM) suggested that the relative importance of these drivers fluctuated over time, indicating temporal compensation of the drivers across time (see Fig. 7). Among

all considered drivers environmental variation was the one that showed the weakest effect on *CS* (Table 2). Additionally, environmental variation had no influence on species synchrony.

Different studies predicted that community structure (Thibaut and Connolly 2013) and functional diversity (Hughes and Roughgarden 2000) are responsible for the stabilization of diverse communities. Here we provide evidence for this prediction and quantify the direction and the relative importance of each driver.

We found that the increase of community evenness as an index of community structure plays a double role in defining the stabilization of the communities, both by directly decreasing *CS* and by increasing synchronous fluctuations and thus indirectly decreasing *CS*. These findings are in line with the role that previous studies attributed to community structure (Isbell et al. 2009; Roscher et al. 2011; Thibaut and Connolly 2013, note however that Thibaut and Connolly (2013) found inconsistent effects of community structure on *CS*). In particular, Roscher et al. (2011) found that species-rich communities that contain more subdominant species and thus have lower evenness were more likely to fluctuate over time due to competition. Increasing species richness therefore can decrease community evenness with the inclusion of multiple subordinate species and, correspondingly, increase stability as a result of the inferior competitive ability of these species.

Our study also clarifies the role of functional diversity. Previous work has been contradictory in predicting effects of functional diversity on *CS*. On one hand, species that are more similar in functional traits are expected to respond in a similar way to environmental changes, and should therefore be synchronous in performance. On the other hand, species that are more similar in functional traits are also more likely to share the same niche space and compete more strongly with each other for common resources. This competition between species can lead to one species outperforming the other at various times and lead to their asynchrony across time (Hughes and Roughgarden 2000). Hence, the direction of the effect that functional trait diversity will have on *CS* seemed, until now, to be

generally difficult to predict. In our study we observed that functional diversity promoted community stability by increasing population asynchrony, and that *FD* was a more predictive measure of *CS* than was *CWM*. This suggests that the dynamics observed in our experiment support the "complementarity effect theory". In contrast, an influence of *CWM* on *CS* would have indicated that the traits of the dominant species were determining community dynamics (Grime 1998; Roscher et al. 2012). Thus, our findings suggest that the stabilization of the communities in the Jena Experiment, happened through niche partitioning which allowed optimization of resources uptake (Loreau 1998; Roscher et al. 2012).

Although previous studies indicated that species can display asynchronous fluctuations in response to environmental variation (Yachi and Loreau 1999), our results show no direct relationship between species synchrony and environmental fluctuation. Instead, we found that functional diversity and community structure reshaped the impact that environmental variations has on species fluctuations. Environmental variations acted directly on the stabilization of communities but not through species fluctuations. This might partially have been due to the measure that we used to detect environmental fluctuation, as we did not quantify responses of individual species to environmental changes. However, because the other investigated drivers already explained a large portion of the total variance in *CS* we believe that a different measure of environmental variation would not have changed the outcome of our study to a large degree.

Finally, our study also highlights the importance of considering an appropriate temporal scale when investigating the mechanisms behind species coexistence in general. We could analyze the patterns of a biodiversity–stability relationship and the role of environmental fluctuation, community structure and functional diversity over ten years. Our findings suggest that different drivers appear to be compensating each other over time (Fig. 7). This could have not been observed in a study of shorter duration or if we would not have measured the different drivers continuously throughout the experiment.

In summary, we demonstrate that not only does species asynchrony stabilize the performance of communities but we also show that the stabilization of more diverse communities might also require time for the underlying mechanisms themselves to stabilize. This work progresses the last decade focused on the role of biodiversity in shaping and maintaining species communities. Specifically, our results shed light on the underlying mechanisms that stabilize species communities. We found that functional diversity, community structure as measured by evenness and species richness are simultaneously responsible for asynchronous species fluctuations. Overall, our results further the understanding about the mechanisms of species coexistence and highlight the importance of considering adequate temporal scales in experimental systems when attempting to understand natural phenomena.

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Tables

Table 1: AIC, R^2 and weights (W_i) for each sequential model. AIC values were obtained from the mixed-effect models, R^2 derived from general linear models without random-effect terms. Weights measure the relative performance of each model with respect to the best one and are calculated as $\mathbf{exp}\left(-\frac{AIC-minAIC}{2}\right) / \sum \mathbf{exp}\left(-\frac{AIC-minAIC}{2}\right)$. *CS* is the coefficient of temporal community stability, *div* is species richness (log-transformed), *sync* is the species synchrony index (transformed), *env* is an index for environmental variation (*env-cv-PC2*), *equit* is evenness and *FD* is functional diversity.

Hypothesis & models	Model	AIC	R^2	W_i
1	CS ~ div	2677	0.056	4.7 e-111
2	CS ~ sync + div	2190	0.515	2.6 e-05
3	CS ~ env + sync + div	2177	0.524	0.02
4	CS ~ equit + env + sync + div	2171	0.528	0.35
5	CS ~ FD + env + sync + div	2175	0.525	0.05
6	CS ~ FD + equit + env + sync + div	2170	0.528	0.58

Table 2: Summary of predictive ability (for community stability, *CS*) of each index individually. The most predictive indices were selected to represent the corresponding driver of variation in *CS*. These terms are given in boldface. For the description of the indices, see "Material and methods".

Index		F-probability for effect on CS	AIC	R^2
Species richness (log-transformed)	**div**	**< 0.001**	**2677**	**0.056**
Species synchrony index (transformed)	**sync**	**< 0.001**	**2201**	**0.331**
Sum of covariances	sum_of_cov	< 0.001	2701	0.030
Sum of realized interactions	C	0.231	2702	0.004
1st principle component of environmental variables	env-PC1	0.937	2706	0
2nd principle component of environmental variables	env-PC2	0.023	2700	0.008
1st principle component of variation in environmental variables	env-cv-PC1	0.979	2706	0
2nd principle component of variation in environmental variables	**env-cv-PC2**	**0.029**	**2701**	**0.007**
Evenness of a plot for the first year of the two-year period	**equit**	**< 0.001**	**2684**	**0.044**
Average evenness of a plot for each two-year period	equit1	< 0.001	2985	0.044
Functional diversity	**FD**	**< 0.001**	**2683**	**0.040**
1st principle component of Community Weighted Mean of traits values	CWM-PC1	0.005	2714	0.010
2nd principle component of Community Weighted Mean of trait values	CWM-PC2	0.640	2722	< 0.001

Figures

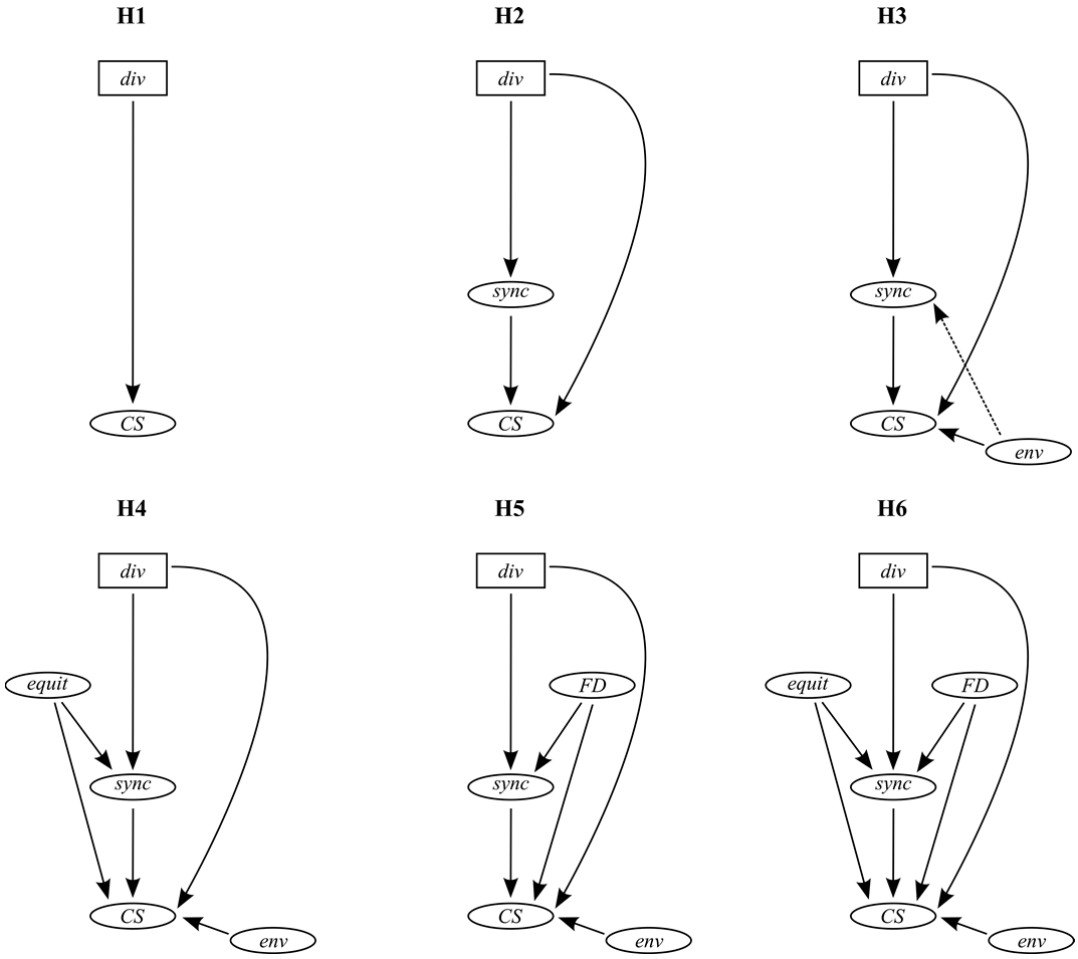


Figure 1: Visual representation of the six hypotheses. Note that in H3, the dotted link between environment and synchrony means we tested for the effect of environmental variations on species fluctuations without finding any.

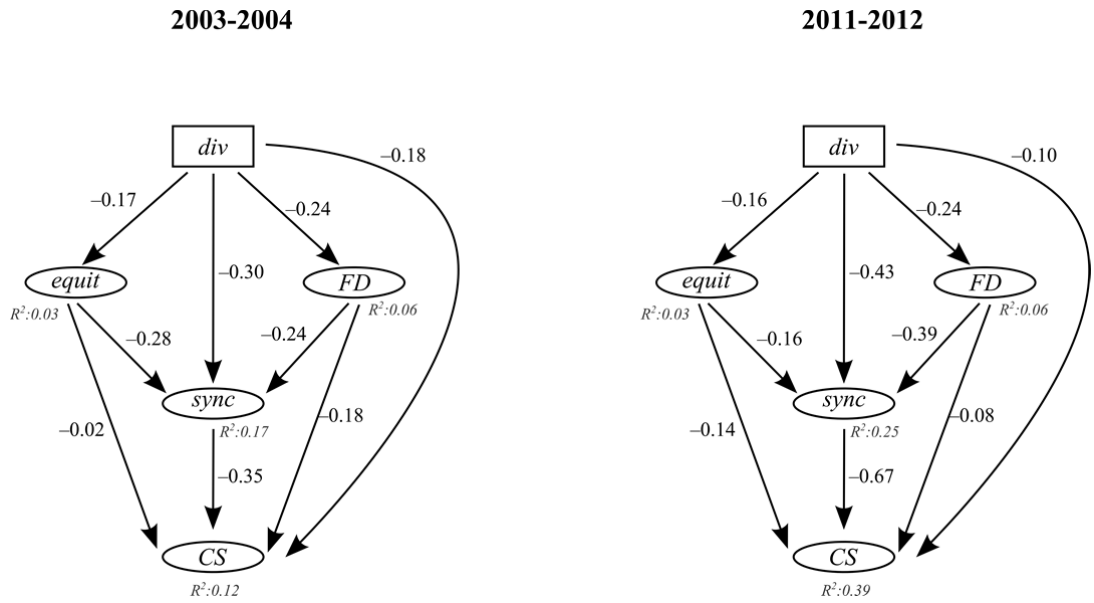


Figure 2: Structural equation model for year intervals 2003–2004 (on the left panel) and 2011–2012 (on the right panel). The endogenous variables are in ellipses and the exogenous variable is in a rectangle. The driver environment has been omitted (see "Material and methods"). We added the paths *div→equit* and *div→FD* because the only exogenous variable here considered is *div*, which was the only variable experimentally manipulated in the experiment. See Table 2 for driver abbreviations.

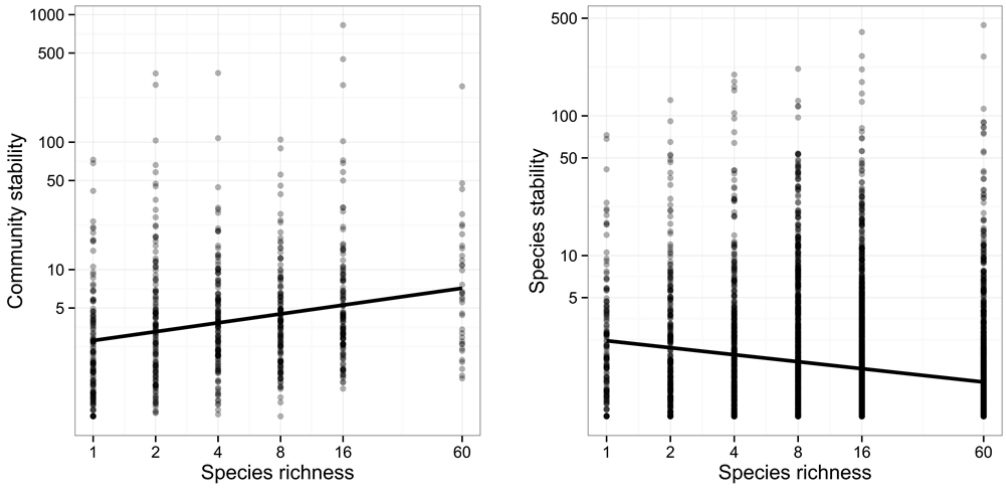


Figure 3: Biodiversity effect on temporal stability of aboveground biomass at the community level (on the left panel) and at the species level (on the right panel). As expected following the insurance effect hypothesis stability increases with species richness at the community level while it decreases at the species level. Both measures of stability are calculated for each time interval from 2003 until 2012. All axes are log-transformed.

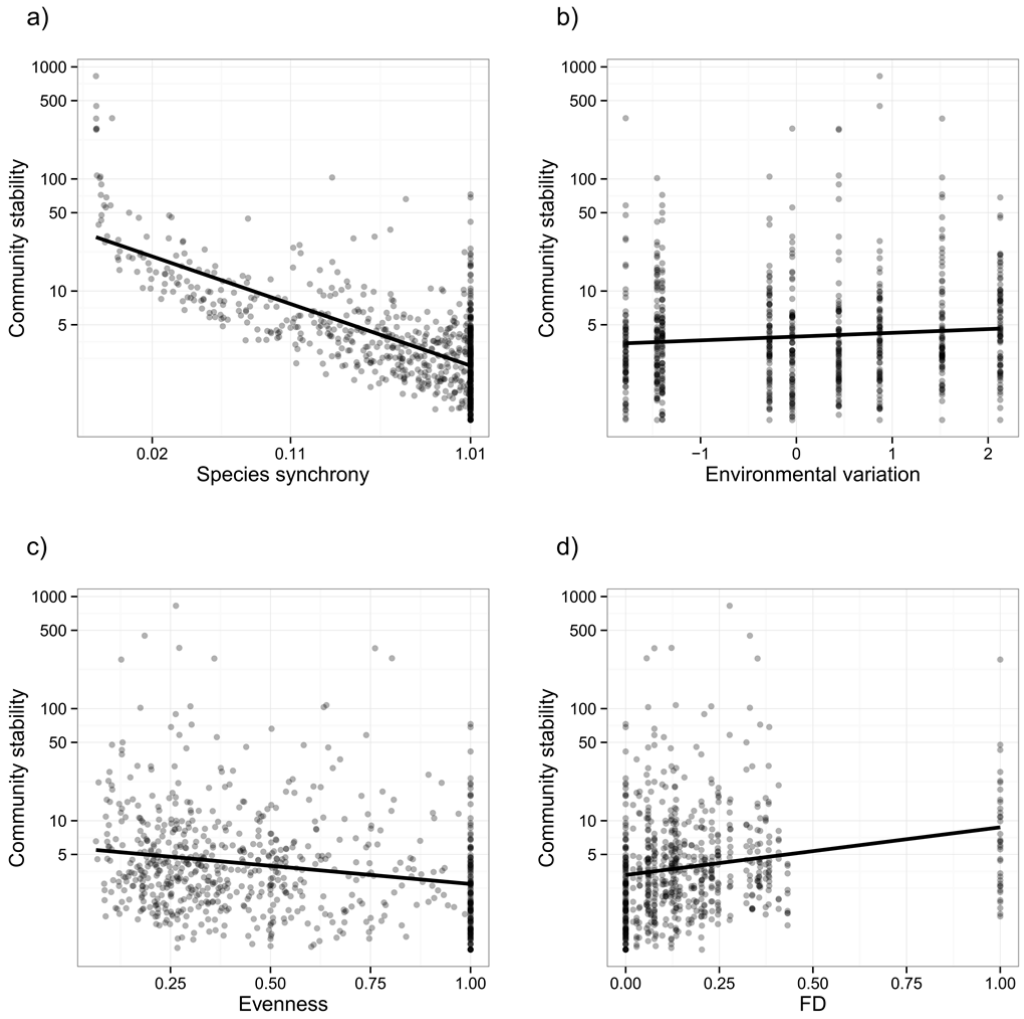


Figure 4: Relationship between drivers and community stability. The relationship between species richness and *CS* is shown in the previous Fig. 3a. The y axis is always $\log_2$-transformed while the x axis is only transformed in 4a (the transformation is log(*sync*+0.01)).

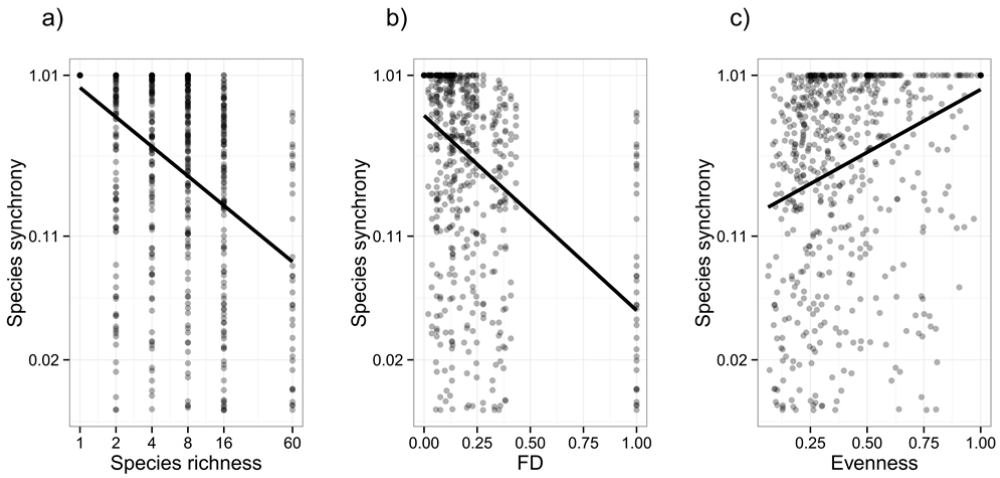


Figure 5: Relationships between species richness (a), functional diversity (b) and evenness (c) and species synchrony (log transformation, log(sync+0.01)). Species richness is on a $\log_2$-scale. Functional diversity and evenness are untransformed.

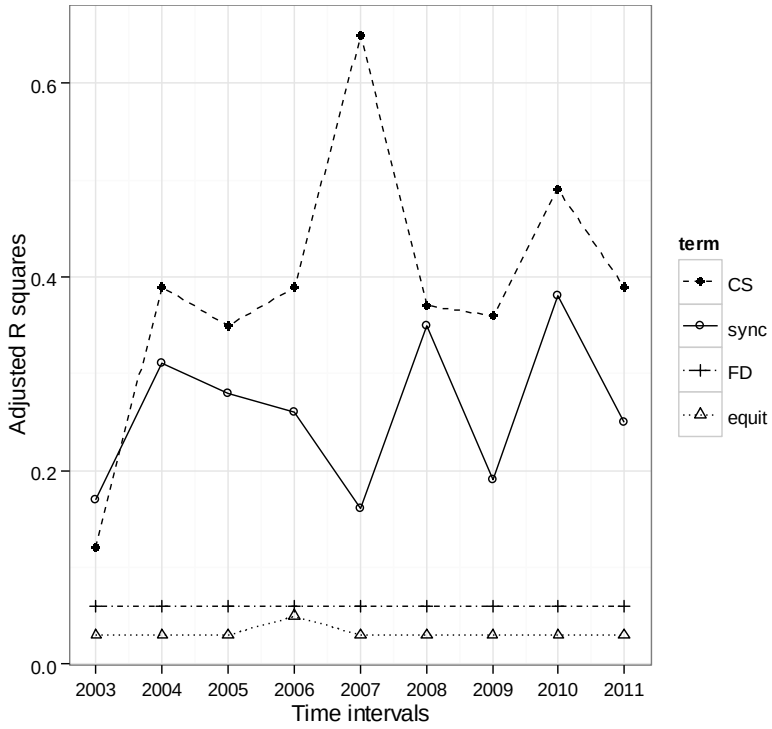


Figure 6: R^2 of the different endogenous terms over time. None of the indices is significantly correlated with time, therefore no slopes are reported. The environmental variation terms are not included (see "Material and methods").

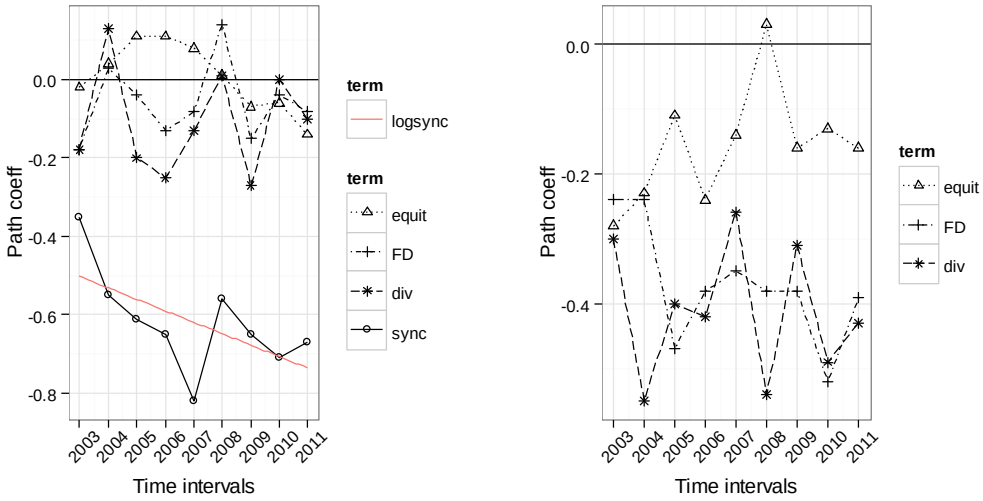


Figure 7: Path coefficients over time: towards *CS* (coefficient of stability) on the left panel and towards *sync* (species synchrony log-transformed) on the right panel. The regression line on the left panel indicates a weak negative relationship over time between *sync* and *CS* ($F_{1, 7} = 4.313$, $P = 0.077$).

Appendix A: Trait data used in the analysis.

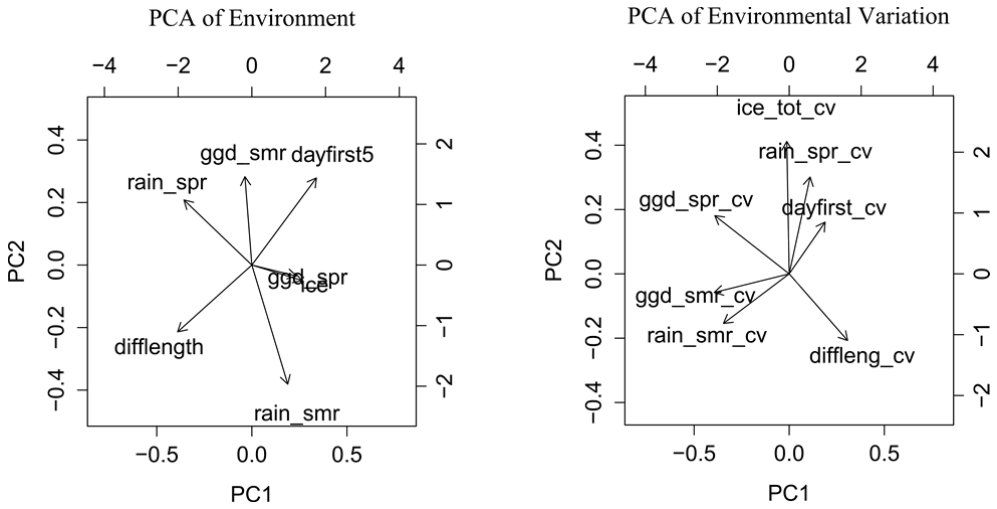
Appendix A: List of functional traits derived from measurements in monocultures of the Jena Experiment and from literature. For further details about the measurements, see Roscher et al. (2012).

Trait name	Trait description	Type of variable (unit)
l.rythm	seasonality of foliage	ordinal
phen.st	start of flowering period	ordinal
phen.dur	duration of flowering period	ordinal
r.type	rooting type	ordinal
r.depth	rooting depth	ordinal
repr.veg	vegetative reproduction	ordinal
life	life cycle	ordinal
m.seed	average seed mass	mg
no.seedling	number of seedlings	m^{-2}
l.shoot	stretched module length	cm
SMF	stem mass fraction	$mg_{stem}\ mg^{-1}_{shoot}$
IMF	inflorescence mass fraction	$mg_{inflorecence}\ mg^{-1}_{shoot}$
SLA	specific leaf area	$mm^2_{leaf}\ mg^{-1}_{leaf}$
d15N.leaf	foliar $\delta^{15}N$	%
d13C.leaf	foliar $\delta^{13}C$	%
N.leaf	leaf nitrogen concentration	$mg\ N\ g^{-1}_{leaf}$
biom.N	biomass:N ratio	$g\ N\ g^{-1}_{shoot}$

Appendix B: Environmental indices

Appendix B1: Abiotic covariates used for the analysis. Seasonal classification was the following: spring = March, April, May; summer = June, July, August; winter = December, January, February. The first seven variables refer to yearly measurements, the second seven variables refer to the variations across two-year intervals in the same variables.

Index name	Index description	Type of variable (unit)
rain_spr	sum of rainfall in the spring months	continuous (mm)
rain_smr	sum of rainfall in the summer months	continuous (mm)
ggd_spr	count of growing degrees days in spring	continuous (count)
ggd_smr	count of growing degrees days in summer	continuous (count)
ice	count of ice days (Tmax < 0°C) in the winter months	continuous (count)
difflengh	number of days between the first and the last day at 5°C	continuous (count)
dayfirst	first day with 5°C (counting from 1st January)	continuous (count)
rain_spr_cv	variation of rain_spr in the given time interval	continuous (sd/mean)
rain_smr_cv	variation of rain_smr in the given time interval	continuous (sd/mean)
ggd_spr_cv	variation of ggd_spr in the given time interval	continuous (sd/mean)
ggd_smr_cv	variation of ggd_smr in the given time interval	continuous (sd/mean)
ice_cv	variation of ice in the given time interval	continuous (sd/mean)
difflengh_cv	variation of difflengh in the given time interval	continuous (sd/mean)
dayfirst_cv	variation of dayfirst in the given time interval	continuous (sd/mean)



Appendix B2: PC axes of the PCA of the environmental indices. On the left panel the seven variables that refer to yearly measurements and on the right panel the seven variables that refer to the variation across two-year intervals are shown. See Appendix B1 for variable abbreviations. PCA analysis was carried out with the *prcomp* function in R and the variables were standardized to have mean zero and unit variance.

CHAPTER 2

How well do pairwise competition trials predict multi-species community assembly and diversity–productivity relationship?

Enrica De Luca, Sebastian Keller, Gian Marco Palamara, Dan F.B. Flynn, Alexandra Weigelt, Markus Fischer, Bernhard Schmid

Abstract

Understanding the mechanisms underlying the coexistence of plants in multi-species communities is important to predict community assembly which in turn affects community productivity. Theoretical studies have used Lotka-Volterra (LV) models to simulate multi-species community dynamics from pairwise competition matrices but no studies ever applied this approach in large multi-species experiments. Here we present such an analysis.

We calculated LV parameters (growth rates, carrying capacities and competition coefficients) from a pairwise competition experiment where all possible 2-species combinations and monocultures of 60 grassland species were planted in pots in three replicates. The parameters were used to run deterministic LV simulations in continuous time and the results were compared with real multi-species communities of originally 1, 2, 4, 8 or 16 species followed over 10 years in a grassland biodiversity experiment in Jena, Germany.

We found that the LV model well predicted realized species richness and community productivity of communities of lower sown diversity in the Jena Experiment. Additionally, the LV models were able to capture to a certain extent also species extinction. Observations and predictions of community properties diverged after the first years of the Jena Experiment. However, the LV models captured some intrinsic characteristics of the communities in Jena, such as the diversity–productivity relationship and the contribution of complementarity, selection and net effects.

Our findings suggest that simple LV parameterization can be used to make realistic qualitative predictions of realized community species richness and productivity at earlier phases of a biodiversity experiment. However, predictions for later years differed more strongly from observed community performances. Thus, interspecific competition holds a crucial role in the establishment of the communities. Other factors such as environmental

variation, trophic interactions and stochastic events may become more relevant in the longer term.

Keywords: biodiversity, community assembly, coexistence, competition, Lotka-Volterra simulation, mechanistic diallel experiment

Introduction

The focus on consequences of biodiversity loss for the functioning of ecosystems (Cardinale et al. 2012; Naeem et al. 2012) has added urgency to understanding the basic mechanisms supporting species coexistence. Species coexistence has been largely explained by two approaches: niche theory, which posits that direct and indirect interspecific competition determines which species can coexist (Tanner et al. 2005; Levine and Hille Ris Lambers 2009) and neutral theory, which rests on historical contingency and the balance of speciation and extinctions to explain coexistence (Hubbell 2001; Bell 2001). Based on niche theory, species-specific characteristics such as differences in growth rates and resource requirements can predict species coexistence and the assembly of communities (Levine and Hille Ris Lambers, 2009; Tanner et al. 2005). Such mechanism can be direct, namely the effects of a neighbor species on a target species, or indirect, namely the effect mediated by a neighboring species which acts on the effect that another neighboring species has on the target species (Weigelt et al. 2007). In contrast, neutral theory posits that interspecific differences have only a limited effect on the assembly of communities while stochastic events are thought to be the driving force (Hubbell 2001; Bell 2001). Studies which tried to disentangle the contributions of one or the other mechanism have typically found greater support for niche-based models (Tanner et al. 2005; Weigelt et al. 2007; Adler et al. 2007, 2010; Levine and Hille Ris Lambers 2009), although no consensus has been reached yet upon the role of species competition in community assembly and stability.

Pairwise competition experiments have been shown to be a useful tool to quantify the role of direct interspecific competition (Connolly et al. 2001; Connolly and Wayne 2005; Weigelt et al. 2007) and to disentangle it from the contribution of indirect interspecific interactions which are not captured by this type of experiments (Wootton 1994a; b; Weigelt et al. 2007; Engel and Weltzin 2008). Pairwise competition experiments and therefore the quantification of direct interspecific competition have often been analyzed with Lotka-

Volterra (LV) models (Grover 1997; Chesson 2000; Dormann and Roxburgh 2005). The LV approach was originally developed to model predator–prey interactions and was later adapted and adopted to predict multi-species community dynamics (Begon et al. 2006). This was mostly done with deterministic LV models using pairwise competition matrices together with species growth rates and carrying capacities (Chesson 2000; Dormann and Roxburgh 2005; de Mazancourt et al. 2013). This approach offers the advantage to evaluate direct interspecific competition without adding any adulteration to the data that might instead originate from the attempt to include such mechanisms as environmental stochasticity and demographic stochasticity (de Mazancourt et al. 2013). Thus, our approach offers a simple Null-model against which more complicated models or real data can be compared.

Different authors have used either LV approaches (Chesson 2000; Cardinale et al. 2004; Dormann and Roxburgh 2005; de Mazancourt et al. 2013) or methods such as competitive hierarchy (Connolly and Wayne 2005; Tanner et al. 2005; Weigelt et al. 2007; Engel and Weltzin 2008) to predict short-terms dynamics of simple communities and found limited evidence that direct interspecific competition explains species coexistence in multi-species communities. However, no study so far tested this in more species-rich communities and over a longer time period. Here we present a study that did exactly this.

We use the LV approach to predict species coexistence and community dynamics observed over 10 years in a biodiversity experiment from pairwise competition coefficients, growth rates and carrying capacities of 60 grassland plant species measured in a 60×60 mechanistic diallel experiment (Schmid and Harper 1985; Schmid and Bazzaz 1994; Schmid et al. 2002; Bossdorf et al. 2004). The species growing in the biodiversity experiment were subject to natural community dynamics where species were affected by a combination of intra- and interspecific competition, indirect species interactions, environmental variation and stochastic events. In contrast, population dynamics of the species growing in the mechanistic diallel experiment were assumed to be more directly affected by interspecific competition. In

the multi-species communities of the biodiversity experiment (Roscher et al. 2004) we measured species composition, realized species richness, community aboveground biomass (= community productivity) over 10 years from 2003–2012. We then used deterministic competitive LV models to predict community dynamics and productivity over time for theoretical communities of the same species compositions as those planted in the biodiversity experiment. The parameters for these LV models were measured in the mechanistic diallel experiment in three replicate blocks. Our results suggest that direct interspecific competition can have a relevant role in the earlier years of establishment of a community, indicating that the use of larger experimental systems and analysis on a long temporal scale are crucial factors to further the understanding of how communities assemble in natural systems.

Material and methods

Experimental design

The data used in this study came from two experiments: a large, long-term field biodiversity experiment, the Jena Experiment (JE), and a mechanistic diallel experiment, here referred to as pairwise competition experiment (PCE). Data from the first experiment, JE, included *observed community properties* (e.g. realized species richness, community productivity). These were compared with *predicted community properties* that we obtained by LV simulation using the data from the second experiment, PCE. For each real community (plot) observed in the JE, three sets of predictions, one from each replicate of the PCE, were obtained. Correspondence between predicted and observed community properties was used as an indication that direct interspecific competition could explain species coexistence and non-correspondence was used as an indication that other factors were more important in affecting species coexistence.

Jena Experiment

The JE was established in 2002 in the flood plain of the river Saale on a formerly arable land (50°55' N, 11°35' E; 130 M above sea level) Jena, Germany. It is currently one of the longest lasting biodiversity experiments in Europe. A pool of 60 grassland species characteristic of meadows of central Europe (*Molinio-Arrhenantheretea,* Ellenberg 1996) was selected to establish communities composed of 1, 2, 4, 8 or 16 species in plots of 20 × 20 m. Each sown diversity level was represented by 16 different species compositions, except for the 16-species level which was only represented by 14 different species compositions (total of 78 plots = communities). All plots were weeded regularly to avoid invasion. However when sown species were going extinct they were not replaced. Aboveground plant biomass harvested in spring was used to represent community productivity. For further details about the field site and specifics of the design see Roscher et al. (2004) and Weigelt et al. (2010).

Pairwise competition experiment

The PCE was setup as follows. First, 1770 pots represented all possible two-species combinations of the 60 species used in the JE ("mixed pots"). In each of the mixed-pots only one individual per species was planted. Second, 60 pots with two individuals of the same species represented all species in monoculture ("mono-2 pots"). Third, 60 pots with one individual only represented all species again, but at half the density of the other pots ("mono-1 pots"). This experimental design was replicated in its entirety three times.

The first replicate (Rep1) was established in a glasshouse in Zurich in 2011. Seeds were obtained from the same company that supplied the JE (Rieger-Hofmann GmbH, http://www.rieger-hofmann.de/). The seeds were planted in multi-tray pots in the glasshouse under controlled abiotic conditions. If necessary for germination, the seeds were treated with gibberellic acid, vernalization or scarification (following Roscher et al. 2004). On 28 March–6 April 2011, individuals were transplanted into pots of size 11 × 11 × 21 cm with a mixture

of sugar beet soil (50%), washed river sand (25%) and perlite (25%). *Anthriscus sylvestris*, *Pastinaca sativa*, *Pimpinella major*, *Ranunculus repens* did not germinate and *Heracleum sphondilium* germinated poorly (50 individuals), therefore not all combinations involving these species could be planted. In total, we obtained 1525 mixed pots, 56 mono-2 pots and 56 mono-1 pots. Aboveground plant biomass was harvested in June and in September at 3 cm above ground, 10 and 22 weeks after planting.

The second replicate (Rep2) was setup in Zurich in 2012, following similar procedure as previously described (minor differences are highlighted in Appendix A). For this replicate it was not possible to grow enough individuals of *Anthriscus sylvestris*, *Heracleum sphondilium* and *Trifolium fragiferum*. Therefore the number of realized pots was 1596 mixed pots, 57 mono-2 pots and 57 mono-1 pots. To simulate field conditions, the pots were moved to an experimental garden in Zurich at the beginning of the spring. Aboveground plant biomass was harvested in June and in September, 10 and 22 weeks after planting.

The third replicate (Rep3) was setup in Bern in 2012 following the same procedure as Rep2. Fourteen species did not germinate (*Ajuga reptans*, *Anthriscus sylvestris*, *Avenula pubescens*, *Geranium pretense*, *Heracleum sphondilium*, *Knautia arvensis*, *Latyrus pratensis*, *Onobrychis vicifolia*, *Pimpinella major*, *Ranunculus repens*, *Sanguisorba officinalis*, *Tragopogon pratensis*, *Trisetum flavescens* and *Viccia cracca*) and three species germinated poorly (*Alopecurus pratensis*, *Pastinaca sativa* and *Poa pratensis*). The total number of pots was therefore 969 mixed pots, 44 mono-2 pots and 45 mono-1 pots. Aboveground plant biomass was harvested in July and in September, 11 and 20 weeks after planting. The aboveground biomass of each replicate was sorted into species, dried at 70°C for 48 hours and weighed. Appendix A gives further details on the setup of the PCE. In total, 4405 experimental pots containing a total of 8652 plant individuals were used in this experiment.

Lotka-Volterra model and application

To simulate population dynamics we used the classic competitive Lotka-Volterra equations (Begon et al. 2006), a system of continuous time deterministic equations describing the rate of change of the biomass of each species in a community of competitors (Case 2000; Dormann and Roxburgh 2005).

For example, in a two species community, the rate of change of the biomass of species 1 in interaction with species 2 is given by

$$\frac{dN_1}{dt} = r_1 N_1 \times \left[1 - \frac{N_1 + \alpha_{12} N_2}{k_1}\right], \quad (1)$$

where N_1 and N_2 are the biomasses of the two species, k_1 (the unit of measure is biomass) and r_1 (the unit of measure is 1/time) are the carrying capacity and the relative growth rate of species 1. The carrying capacity k_1 is the maximum population size of species 1 growing alone in a given environment. The coefficient α_{12} (dimensionless) is the interaction coefficient of species 2 on species 1 i.e. the per capita effect of species 2 on species 1. If $\alpha_{12} > 0$ species 2 is a competitor of species 1, while if $\alpha_{12} < 0$ species 2 is a facilitator for species 2. Equation (1) describes the dynamics of species 1 and is coupled with a symmetric equation for species 2.

When there are more than two species in the community, equation (1) can be generalized to

$$\frac{dN_i}{dt} = r_i N_i \times \left[1 - \frac{N_i + \sum_{i \neq j}^{S} \alpha_{ij} N_j}{k_i}\right], \quad (2)$$

where *S* is the number of species in the community and α_{ij} is the per capita effect of specie *j* on species *i*. Equation (2) represents a system of *S* differential equations, one per species. The dynamics of the species' biomasses are completely determined once the vector of growth rates (r_i, with *i*=1,…,*S*), carrying capacities (k_i, with *i*=1,…,*S*) and the *S*×*S* matrix of

interspecific interactions is given together with the initial conditions for the species' biomasses.

For each species we calculated the carrying capacity as the mean harvested biomass of pots mono-1 and mono-2. A set of k_i was measured separately from each replicate of the PCE.

The relative growth rate r_i is the maximum rate with which the biomass of species *i* increases in a given time interval if grown alone in a given environment. For each species we calculated it as:

$$r_i = \frac{log(n_i+1)-log(1)}{t_2-t_1}, \quad (3)$$

where n_i is the aboveground biomass of species *i* in mono-1 pots at the second harvest and $t_2 - t_1$ is the number of days between the first and the second harvest. We used a correction term of 1 g to represent a constant non-harvested biomass (biomass below 3 cm) and *log(1)* the aboveground biomass of species *i* at the first harvest. We considered the time $t_2 - t_1$ because we meant to quantify the time to reach equilibrium from the last common harvest. It is however arguable that also the time $t_2 - t_0$ could have been used. A set of r_i was measured separately from each replicate of the PCE.

A 60 × 60 matrix of interactions was calculated from each replicate of the PCE. The interspecific interaction coefficient was calculated as:

$$\alpha_{ij} = \frac{k_i - N^*_i}{N^*_j}, \quad (4)$$

where N^*_i and N^*_j are the biomasses obtained setting dN_i/dt and dN_j/dt to zero in equation (1).

From each replicate of the PCE we derived a set of Lotka-Volterra parameters for each species composition (plot) in the JE: a matrix of interspecific competition coefficients, a vector of carrying capacities and a vector of growth rates. As the LV equation models species

coexistence, in each replicate we excluded from the matrix of α_{ij} all combinations where one of the two species went extinct in a species pair ($\alpha_{ij} = +\infty$ or $\alpha_{ij} = -\infty$). Furthermore, we also excluded from the competition matrix all species for which we were not able to measure carrying capacity. For some plots in the JE we therefore could only model subsets of the originally planted communities for some replicates of the PCE. In these cases we adjusted the sizes of the vector of carrying capacities and the vector of growth rates to the size of the matrix of the subset. We predicted community properties only for those communities where the species in the predicted subset accounted for at least 90% of the aboveground productivity of the entire community in the JE. The total number of observed (in JE) and predicted (from the PCE) communities used in the analysis thus was reduced to those for which values from the PCE were available for the particular replicate and year to be predicted.

Analysis

We compared observed community properties from the JE during 10 years (2003–2012) with predicted community properties calculated from each replicate of the PCE. First, we compared the following predicted and observed community properties for each species composition (plot) in the JE: realized species richness and species extinctions. For species extinction we counted predicted species extinctions that were not observed ($ext_{overpredict}$), observed species extinctions that were not predicted ($ext_{underpredict}$) and correctly predicted extinctions ($ext_{correct}$). Predicted realized species richness was quantified as the number of predicted species with biomass > 0.001 g (the lowest measure on the scales used both in JE and in PCE for weighing biomass), and observed realized species richness was measured as the number of observed species with biomass > 0 g. Further explanations of $ext_{overpredict}$, $ext_{underpredict}$ and $ext_{correct}$ are given in the supplementary material (Appendix B.1). To test whether predictions of extinctions were different from random predictions, we took 100

random samples for each replicate of the PCE following two procedures. That is, for each community in each year and for each replicate, we i) randomly sampled 100 species sets of the same number of species as we observed going extinct and compared their composition with the one of the species set that we predicted to go extinct and ii) randomly sampled 100 species sets of the same number of species as predicted going extinct and compared their composition with the one of the species set that we observed to go extinct (Appendix B.1). In both cases, we counted the number of species that overlapped the sampled and the predicted (i) or the sampled and the observed (ii) values and we compared them to $ext_{correct}$.

Next, we compared predicted and observed community productivity. Predicted community productivity was calculated from each replicate of the PCE for ten years. Similarly, observed community productivity was measured for each year of the JE (2003–2012).

Finally, we compared observed and predicted community structure and diversity–productivity relationships. The measures of community structure that we used were the Jaccard index and the Morisita-Horn index. The Jaccard index (Greig-Smith 1983) focuses on the number of shared species between observed and predicted communities:

$$J = \frac{N_{a,b}}{N_{a,b}+N_{0,b}+N_{a,0}}, \tag{5}$$

where $N_{a,b}$ is the number of shared species, $N_{0,b}$ are species present in community b but not in community a and $N_{a,0}$ are species present in community a but not in community b. The Morisita-Horn index of dissimilarity (Morisita 1959; Horn 1966) additionally accounts for species abundances:

$$MH = \frac{2\sum(an_i \times bn_i)}{\left(\frac{\sum an_i^2}{aN^2}+\frac{\sum bn_i^2}{bN^2}\right)aN \times bN}, \tag{6}$$

where an_i and bn_i are the biomasses of species in community a (e.g. observed species biomass) and community b (e.g. predicted species biomass), and aN and bN are the realized diversities of community a and community b. Both indices range from 0 to 1, where 0 is

maximum dissimilarity and 1 maximum similarity. To compare the diversity–productivity relationship between observed and predicted communities we used sown species richness and community productivity and the additive partitioning terms Net Effect (NE), Complementarity Effect (CE) and Selection Effect (SE) (Loreau and Hector, 2001).

All analysis were done with the Software R v3.0.2 (R Development Core Team, http://www.R-project.org; deSolve 1.10-8 for LV simulation).

Results

Identification of potential experimental errors

We first verified that the results obtained were not biased by possible experimental errors. Our analysis showed that rank-abundance distributions of monocultures in the Jena Experiment (JE) were different from rank-abundance distributions of both mono-1 and mono-2 pots in the pairwise competition experiment (PCE) (Appendix C). This suggests that species performances in one system may not resemble performances of the other system. Similarly, rank-abundance distributions of mixed communities in the JE were different from rank-abundance of mixed pots in the PCE (Appendix C). On the other hand, predictions of monoculture productivity and observations of monoculture productivity where highly comparable (see Results section: *Comparison of predicted and observed species richness and extinctions*).

Biomass production in mono-1 and mono-2 pots did not differ from each other across all replicates. This indicated that species growing as single-individual monocultures in the PCE had reached a peak of biomass production. The first and the second replicate of the PCE allowed more complete estimations of parameters for the LV models and therefore prediction for more communities in the JE (total number of predictions: 456 from Rep1, 590 from Rep2 and 55 from Rep3 compared to a maximum of 774 as 78 communities were measured 10

years minus two monocultures abandoned in year 2010). In particular, from Rep3 we did not obtain any predictions for 16-species communities and only one prediction in one year for 8-species communities (Appendix D.1).

Comparison of predicted and observed species richness and extinctions

LV-predictions of realized species richness were more similar to observations of realized species richness during earlier years of the JE than during later years (Fig. 1). In particular, predicted and observed realized species richness were significantly correlated only for 2- and 4-species plots in 2003 ($P < 0.05$) but not for higher species richness or later years ($P > 0.05$). In 2003, predictions and observations of realized species richness were similar and prediction were more accurate at lower than at higher level of sown diversity (prediction ~ observation realized diversity slope = 0.61, $P < 0.05$). Predicted and observed realized species richness in monocultures were identical; this however is ascribable to the fact that LV does not account for extinctions in monocultures. For this reason monocultures were not included in further comparisons of realized species richness.

Predicted realized species richness was always lower than observed realized species richness (Fig. 1). The model predictions from the PCE captured on average at least ~50% of the realized species richness for the diversity levels 2, 4 and 8-species plots across the 10 years of the experiment (Appendix D.2). However, predicted and observed species identities diverged; thus, predicted realized species richness adjusted for the number of species both predicted and observed (correct predictions) showed a larger divergence than just species richness (Appendix D.2). This finding might be influenced by the fact that predicted realized species richness in every sown diversity level tended to reach a plateau after two or three simulated years (mean and standard error for years 2006–2012: 1.57 ± 0.04 species for sown diversity level 2; 2.33 ± 0.05 species for sown diversity level 4; 3 ± 0.07 species for sown

diversity level 8 and 3.63 ± 0.11 species for sown diversity level 16). This resulted from the deterministic LV-approach where species do not fluctuate after reaching equilibrium.

We correctly predicted the majority of extinctions, except in communities of sown diversity level 2 (Fig. 2 and details on the different replicates in Appendix B.2). The mean proportion of correct number of predicted species extinctions to the number of observed species extinction increased with increasing sown diversity level (mean ± standard error for sown diversity level 2, 4, 8 and 16: 0.12 ± 0.06, 0.56 ± 0.04, 0.71 ± 0.03, 0.80 ± 0.02). No clear temporal pattern in predictions of extinctions was found (Table 1). However, as the number of predicted species extinctions was higher than the number of observed species extinctions, we tested that the increased proportion of correct predictions was not only a consequence of this. We randomly sampled a number of species equivalent to i) the number of predicted extinctions and ii) the number of observed extinctions, and we compared them with Lotka-Volterra predictions (see Material and Methods). The results showed that, except in communities of sown diversity level 2 where the mean of Lotka-Volterra correct predictions ($ext_{correct}$) corresponded to the mean of the random samples of prediction (values of 1 in Fig. 3), $ext_{correct}$ was always higher than the mean of the random samples of predictions (values below 1 in Fig. 3). However, these were not significantly different (proportions of random samples larger than the mean of $ext_{correct}$ was always higher than 0.05). Random samples of observations and random samples of predictions gave similar results in terms of proportions of random samples larger than the mean of $ext_{correct}$ and also did not show any clear temporal pattern (Fig. 3).

Comparison of predicted and observed community productivity

We found that predicted and observed community productivity were more comparable in the first years rather that in later years of the JE. In particular, mean of predicted and observed monoculture productivity in year 2003 and 2004 were similar (mean total predicted / mean

total observed community productivity in the two years was 337/311 g/m^2 and 373/389 g/m^2, Fig. 4), however, non comparable at the community level ($P > 0.05$). Predicted community productivity was higher overall than observed community productivity for each sown diversity level across time. Additionally, in the later years of the JE the dissimilarity between predicted and observed community productivity was larger at lower diversity levels than at higher ones (Fig. 4). However, at higher initial diversity levels the discrepancy in realized species richness between predicted and observed species richness was larger (see above) and this might have had a compensatory effect on community productivity (see below).

Comparison of predicted and observed community species composition and diversity–productivity relationship

Species composition based on a presence-absence index increased in dissimilarity between predicted and observed communities at higher sown diversity levels (Jaccard Index mean ± s.e. for sown diversity levels: 2 = 0.59 ± 0.03; 4 = 0.59 ± 0.02, 8 = 0.42 ± 0.01 and 16 = 0.27 ± 0.02). This trend was similar when considering abundances, although similarities were overall lower compared to presence-absence index values (Morista-Horn index mean ± s.e. for sown diversity levels: 2 = 0.35 ± 0.02, 4 = 0.30 ± 0.02, 8 = 0.21 ± 0.02 and 16 = 0.05 ± 0.02).

The diversity–productivity relationship in predicted communities and observed communities were comparable on a log scale (Fig. 5). The predicted diversity–productivity relationship was above the observed one, due to LV overestimation of community productivity (+216 g/m^2 for monocultures, + 360 g/m^2 for diversity level 2, + 434 g/m^2 for diversity level 4, + 486 g/m^2 for diversity level 8 and + 935 g/m^2 for diversity level 16).

The complementarity effect (CE) calculated for predicted communities increased and the selection effect (SE) decreased with increasing diversity levels and the same qualitative results were observed in the JE (Fig. 6). Additionally, this pattern was constant across the 10

years of the JE. For the predicted communities this constancy partially derives from the deterministic LV-model in which simulated communities reached equilibrium status quite rapidly (Fig. 4).

Discussion

We showed that predictions of community assembly and partially of productivity, based on LV-parameters obtained from a pairwise competition experiment, were most accurate for the initial years of observed real communities in a field experiment. Our results suggest that the role that interspecific competition plays in shaping coexistence might have been underestimated in previous studies.

Potential intrinsic limitations of predictions

Discrepancies between predicted and observed community properties indicate that the Null-model, which explains these properties purely from pairwise interspecific competition, is not sufficient to capture the whole biological reality. Before we discuss biological factors that might have caused these discrepancies, we discuss potential methodological factors that might also have influenced discrepancies between predictions and observations. First, our mechanistic-diallel experiment (PCE) to estimate LV-model parameters was carried out with new seed material and in a different environment than was the case for the biodiversity experiment (JE) in which the real communities were observed. This potentially led to differing species ranks between the two experiments (see Appendix C), as also obtained in previous studies (Wilson and Keddy 1986; Karez 2003; Engel and Weltzin 2008). Despite these differences we argue that predictions of community properties from the LV model were reliable because i) plant growth in the PCE resembled the growth in the JE, and ii) the LV-assumptions for the validity of the model were met. Below we explain these two points.

First, despite different rank-abundance distribution among the two experiments, the 60 plant species used in the study had comparable mean aboveground biomass in monocultures (see Fig. 4) suggesting that individual species in the JE and in the PCE showed similar growth. Second, the LV-approach assumes equilibrium conditions, meaning that plants in the PCE reached a stable production of biomass at the time of the harvest (Begon et al. 2006). Indeed, we found that at this time monocultures with one individual and with two individuals had reached the same constant final yield in the majority of the monocultures pots and therefore the equilibrium condition was fulfilled. However, this does not guarantee that mixtures also reached equilibrium at this time (Dormann and Roxburgh 2005) as they actually had even larger aboveground biomass yields than monocultures (the net effect NE in the PCE experiment was positive for 561 out of 755 mixtures). Thus, whereas carrying capacity and competition coefficients seemed to be well estimated at equilibrium, the greater difficulty was to measure the maximal relative growth rate of the 60 species in monocultures. On the one hand, we did not know the initial size of the plants and on the other hand, we could estimate the next to initial size after a time interval only from aboveground biomass and had no information about the size of the root system. These inaccuracies in measuring growth rates might have led to overestimation of maximal relative growth rates of species and, as a consequence, to the overestimates of community productivities.

Comparing predicted and observed community properties

We found that predicted and observed community properties were more comparable in early years of the JE both in qualitative and in quantitative terms and these results were evident particularly for communities of low sown diversity levels. From a quantitative perspective, predicted community productivities were generally higher than observed ones, possibly due to an overestimation of relative growth rates of species (see previous section). In contrast, predicted values were lower than observed ones for realized species richness. The decrease of

observed community productivity over time could not be predicted by the LV-simulations which was not surprising and suggests that this decrease was due to other biological factors such as resource depletion (e.g. Olff and Bakker 1991; Roscher et al. 2008) or accumulation of pathogens (Klironomos 2002; Marquard et al. 2013). Obviously, our LV-approach did not consider such effects. Regarding the underestimation of realized species richness by the LV approach, environmental fluctuations changing the LV-parameters over time in the real-world situation may have allowed more species to coexist than would be possible under constant environmental conditions at equilibrium. In fact, the insurance hypothesis (Bai et al. 2004; Ives and Carpenter 2007) suggests that species coexist in more diverse communities because their constituting populations fluctuate (Flynn et al. 2008; Schmid et al. 2008; Isbell et al. 2009, De Luca et al. *in preparation*). The deterministic LV-approach can not capture these predictions of the insurance hypothesis.

Our findings were to a certain extent unexpected: previous research showed that mechanisms of indirect interspecific competition and stochasticity determine species coexistence whilst the role of direct interspecific competition is limited (Case and Bender 1981; Wootton 1994a; b; Grover 1997; Tanner et al. 2005; Dormann and Roxburgh 2005; Weigelt et al. 2007; Adler et al. 2007; de Mazancourt et al. 2013). Also, there is broad scientific evidence that indirect interspecific competition and stochasticity are neither captured by mechanistic diallel experiments (Connell 1983; Schoener 1983; Engel and Weltzin 2008) nor by LV models (Case and Bender 1981; Grover 1997; Chesson 2000; Dormann and Roxburgh 2005). Thus, while we expected to have a larger discrepancy between predicted and observed community properties, we found instead that we could well predict some community properties in the first years of the Jena Experiment and at low sown diversity. Thus, we suggest that direct interspecific species competition influences the establishment of the species especially in communities of low sown diversity. These results were comparable to those of Weigelt et al. (2007) who observed that predicted and observed

community properties were generally comparable at low species richness (4 species). Although in their study non-additive mechanisms (i.e. indirect interspecific competition and stochasticity) occurred in specific species combinations, predictions met the observations, suggesting that the role of direct interspecific competition might be linked to the considered spatial scale (Weigelt et al. 2007). Thus, both our study and the study of Weigelt et al. (2007) emphasize the necessity of considering broad temporal and spatial scales when predicting species coexistence; overlooking adequate scales might have led to the underestimation of the role of interspecific competition. The few other studies that investigated the temporal changes of the mechanisms of species coexistence considered in fact a smaller time scale than ours (Connolly and Wayne 2005; Engel and Weltzin 2008; de Mazancourt et al. 2013).

The different mechanisms of species coexistence are likely to change in importance along the temporal scale. In our study, direct interspecific competition influences the establishment of species in low sown diversity communities during the initial years of the field experiment. Later, direct interspecific competition loses importance. Therefore, the successful establishment of one species rather than another seems to be driven mostly by its competitive ability, measured as the direct interaction with its neighbor. These mechanisms seem to happen during the establishment of also the more diverse communities, however with lower intensity, where multispecies interactions would be derived from the sum of all pairwise interactions. After the communities established, indirect inter- and intraspecific competition and stochasticity mechanisms become predominant in defining species coexistence. Recent findings suggest that evolutionary and co-adaptive mechanisms might also be at play during the later stages of the community development (Zuppinger-Dingley et al. 2014), thus justifying the predominant role of interspecific competition only in the early phase of community establishment.

In order to understand to which extent LV models were able to capture intrinsic characteristics of the JE communities, we also compared LV predictions and random

predictions of species extinction, predicted and observed species composition, diversity–productivity relationship and additive partitioning terms. We found that indeed LV prediction of extinctions were better than random predictions (see Fig. 3), but the difference between LV predictions and random predictions was not supported by statistical evidence (the proportion of random predictions larger than the mean of LV predictions of extinctions was > 0.05). Additionally, the predicted and observed community compositions were dissimilar (Jaccard index and Morista-Horn index). The evaluation of the capability of LV-models to predict both extinctions and community structures suggests that PCE might not be able to capture intrinsic properties of the JE communities. However, we also observed that both predicted CE, SE and NE and predicted diversity–productivity relationship were comparable to the observed ones. These last findings suggest instead that PCE might be able to capture the intrinsic characteristics of JE communities and that the additive partitioning terms and the diversity–productivity relationship might be driven by direct interspecific competition. Thus, deterministic LV models, despite their unsuccessful prediction of some community characteristics, can be a useful tool to predict the shape of the diversity–productivity relationship and the strength of the mechanisms of complementarity and selection effect that regulate it.

In summary, our work suggests that different mechanisms play a role in defining species coexistence. Specifically we show that the role of direct interspecific competition should not be underestimated since it appeared to be important in earlier phases of community establishment. Our experimental approach was rather robust and solidly based on measures form experimental setups and it led to higher than expected comparable predicted and observed community properties relative to previous findings. Thus, our results highlight the need to use adequate temporal and species scales. We therefore suggest that future studies on

species coexistence should consider large spatial-temporal scales in order to translate results from experimental scales to natural systems.

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Tables

Table 1: Mean of correct predictions of extinctions / observed extinctions ($ext_{correct}/(ext_{correct} + ext_{underpredict})$) for the three replicates of the PCE, sown diversity level and year. For plots where the total observed extinctions ($ext_{correct} + ext_{underpredict}$) and total predicted extinctions ($ext_{correct} + ext_{overpredict}$) were 0, proportions were given the value of 1 instead of infinite in order to include them in the averaging. Dashes represents that no predictions could be made.

	Rep1				**Rep2**				**Rep3**		
	Initial species richness				***Initial species richness***				***Initial species richness***		
Year	**2**	**4**	**8**	**16**	**2**	**4**	**8**	**16**	**2**	**4**	**8**
2003	1	0.68	0.66	1	0.86	0.80	0.77	0.87	1	-	-
2004	1	0.63	0.61	0.67	1	0.75	0.48	0.87	1	-	-
2005	0.78	0.55	0.74	1	0.78	0.73	0.79	0.75	1	1	-
2006	0.88	0.52	0.72	1	0.89	0.53	0.82	0.74	-	-	-
2007	0.88	0.50	0.90	1	0.88	0.50	0.72	0.83	-	-	-
2008	0.78	0.83	0.67	0.79	0.78	0.42	0.76	0.61	1	1	-
2009	1	1	0.58	0.76	1	0.88	0.77	0.78	-	-	-
2010	0.89	0.69	0.78	0.82	0.88	0.64	0.69	0.85	-	0.5	-
2011	0.63	0.86	0.70	0.82	0.56	0.30	0.72	0.76	-	-	-
2012	0.63	0.73	0.60	0.76	0.70	0.67	0.70	0.82	-	-	0.75

Figures

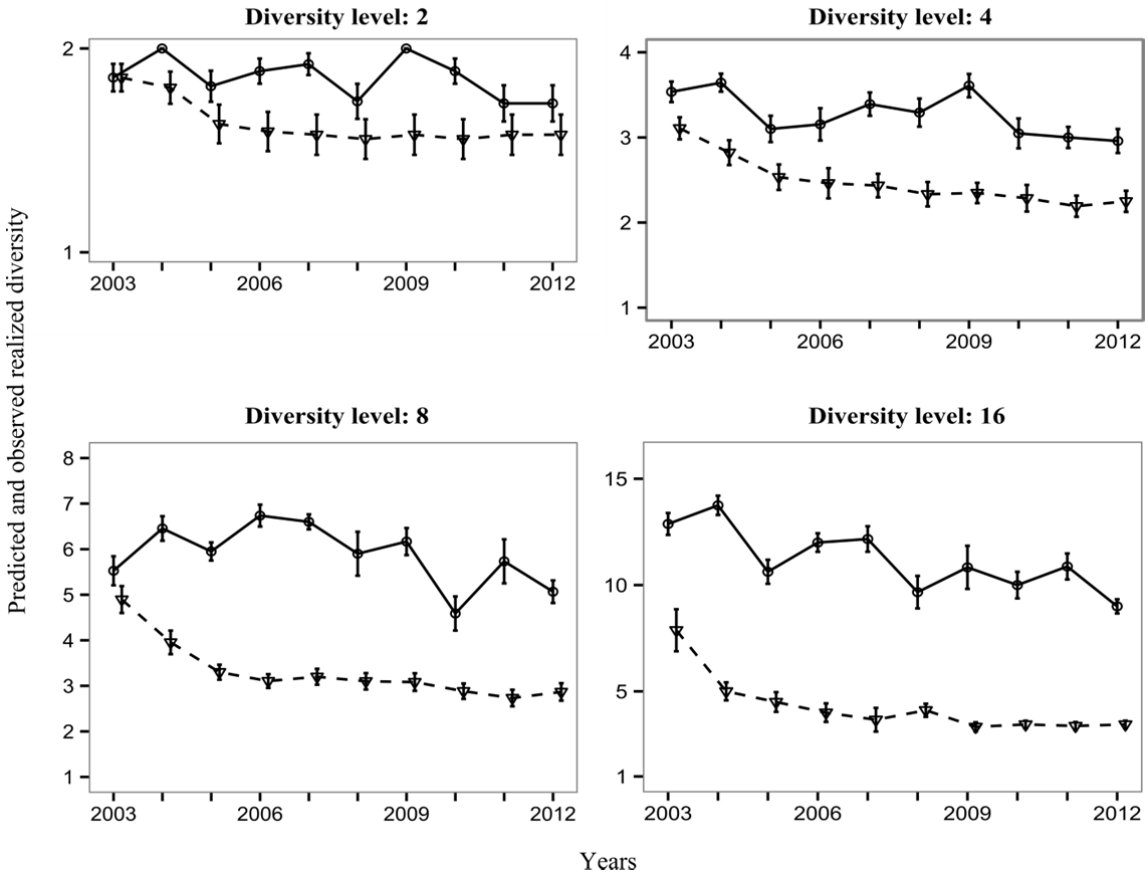

Figure 1: Means ± 1 standard error of observed (full line and circles) and predicted (dashed lines and triangles) realized species richness over the ten years of the Jena Experiment. The four panels are for the four levels of sown (initial) species richness in a community, 2, 4, 8 and 16

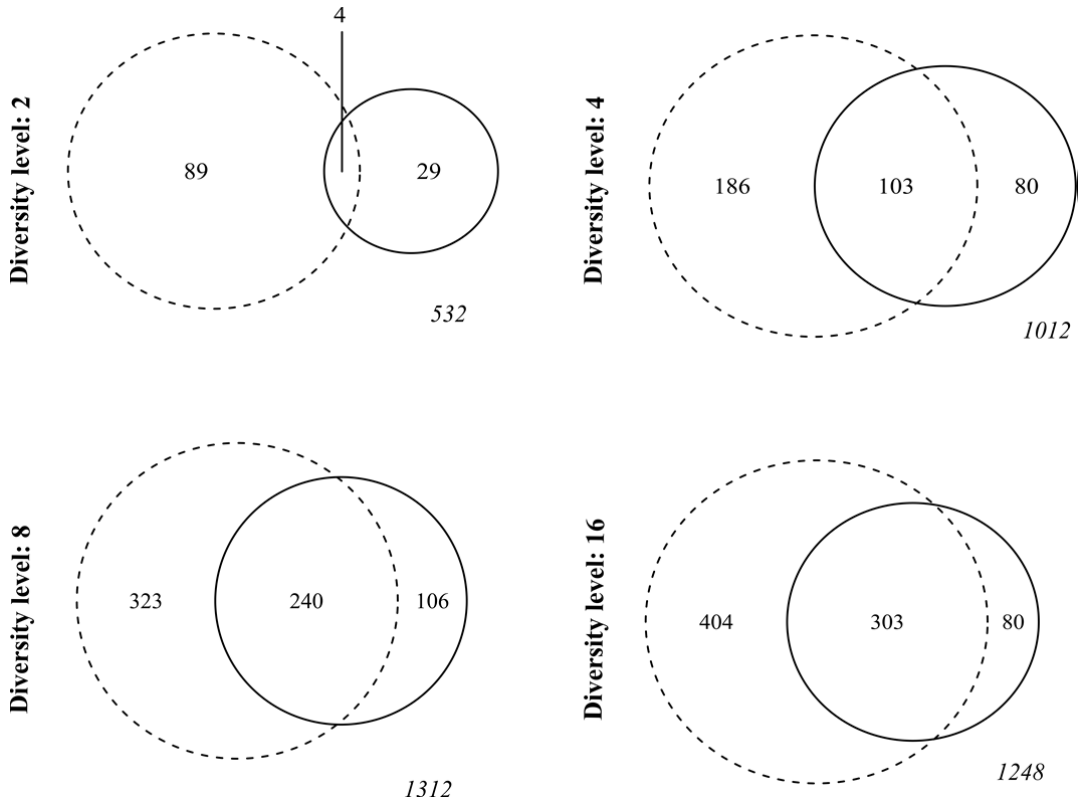

Figure 2: Venn diagrams illustrating the total number of extinctions observed (full line) and predicted (dashed line) in each diversity level. Data are pooled across the three replicates of the pairwise competition experiment. Numbers in italics are the maximum number of species which could go extinct, namely sown species richness × number of predicted communities × number of years. See Appendix B.2. for details about the contribution from each replicate of the pairwise competition experiment. The four panels are for the four levels of sown (initial) species richness in a community, 2, 4, 8 and 16.

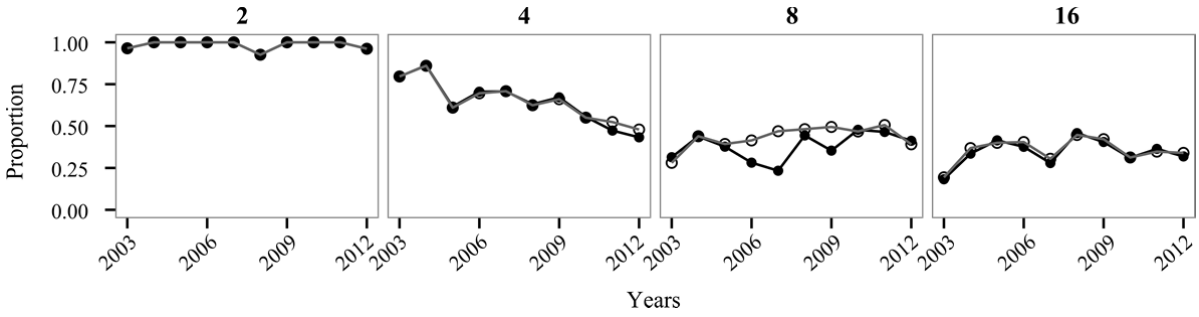

Figure 3: Changes over time of proportions of random sample of predictions ≥ the mean of $ext_{correct}$ (full circles and black line) and random sample of observations ≥ the mean of $ext_{correct}$ (empty circles and grey line). Since there are no values above 1 (i.e. number of correct random prediction > number of correct LV prediction) we deduct that LV predictions are always better than random ones. The four panels are for the four levels of sown (initial) species richness in a community, 2, 4, 8 and 16.

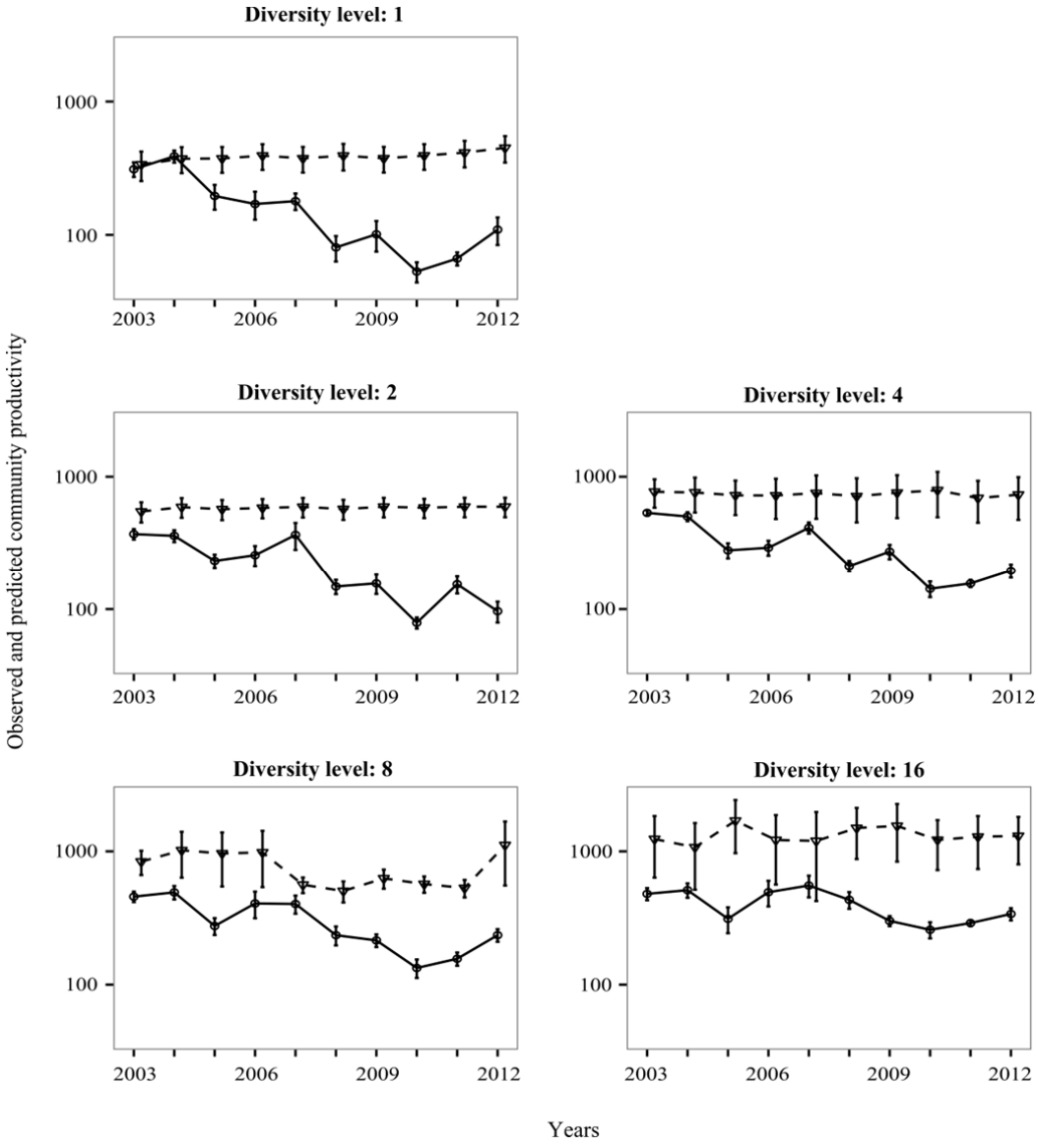

Figure 4: Means ± 1 standard error of observed (full line and circles) and predicted (dashed lines and triangles) community productivity (g/m^2) on a log scale over years. The five panels are for the five levels of sown (initial) species richness in a community, 1, 2, 4, 8 and 16.

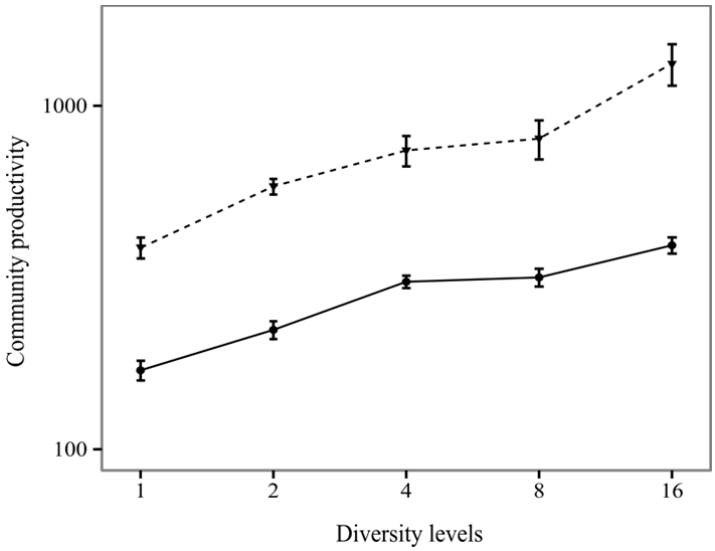

Figure 5: Species richness−productivity relationships for observed (circles and full line) and predicted community productivity (triangles and dashed line). The data are pooled for all years as the shown relationship was similar over time. Community productivity is in g/m2 on a log scale. Means and standard errors are indicated by symbols and vertical bars, respectively.

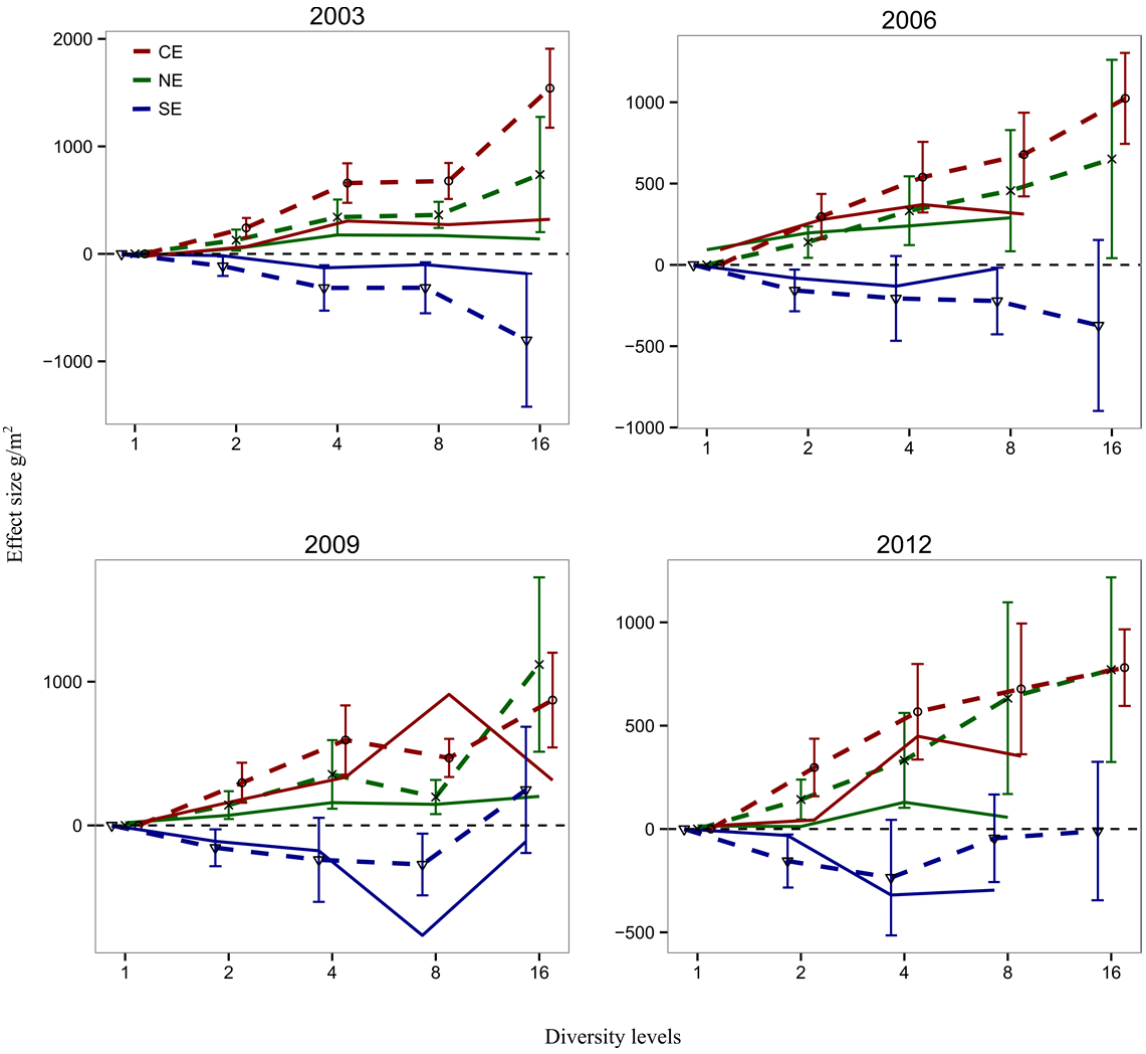

Figure 6: Additive partitioning of predicted community productivity (from PCE) and observed community productivity (from JE) in four years. Means ± 1 standard error of complementarity effects (red, CE), selection effects (blue, SE) and net effects (green, NE) are shown for predicted (dashed lines) and observed communities (solid lines). Data of predicted communities are pooled for all experimental replicates. Missing additive partitioning terms of the JE in year 2006 and year 2012 are due to missing monocultures in the JE: additive partitioning was calculated for those JE mixtures where all species yielded biomass in monoculture.

Appendix A

Pairwise competition experiment

First replicate

The first replicate was established in the Greenhouse of the University of Zurich, Switzerland. Seeds of the sixty plant species were germinated in February 2011 in the greenhouse under controlled abiotic conditions (light from 7:00 to 19:00, light intensity 15 klx if outside was lower than 20 klx, temperature range 16°C (daily maximum)–8°C (night minimum), and daily watering). Gardening peat soil (GVA, Zurich, Switzerland) was used for germination. We changed abiotic conditions after 15 days to encourage plant growth (light from 7:00 to 19:00, temperature range 20°C (daily maximum)–17°C (night minimum), and watering every third day). Plant individuals were transplanted into multi-pot trays one individual per plug to allow each individual to grow under the same conditions (from 14.03.2011 to 23.03.2011). Abiotic conditions were gradually adjusted to reach more comparable conditions to spring conditions (light from 7:00 to 19:00, light intensity 15 klx if outside was lower than 20 klx, temperature range 18°C (daily maximum)–12°C (night minimum), and watering every third day). All species were then transplanted into plastic pots of 11 × 11 × 21 cm (from 28.03.2011 to 06.04.2011).

Second replicate

The second replicate of the experiment was established in Zurich in 2012 following the procedure described above. Individual species were grown as one individual per plug in the multi-pot trays (therefore did not need an intermediate transplanting phase) and transplanted into the plastic pots at the end of April 2012. The pots were moved from the greenhouse to the experimental garden of the University of Zurich in late April 2012 and watered daily.

Third replicate

The third replicate took place in Bern in 2012 followed the same experimental procedure as the second replicate. Plants grew under greenhouse controlled abiotic conditions and were

moved to the experimental garden of the University of Bern, Switzerland. The soil utilized, in contrast to the two previous experiments, was a mixture of low lime, sand and humus, called "'Rasentragschicht AarGround'" from Aarekies Brienz AG (Bern, Switzerland).

Appendix B

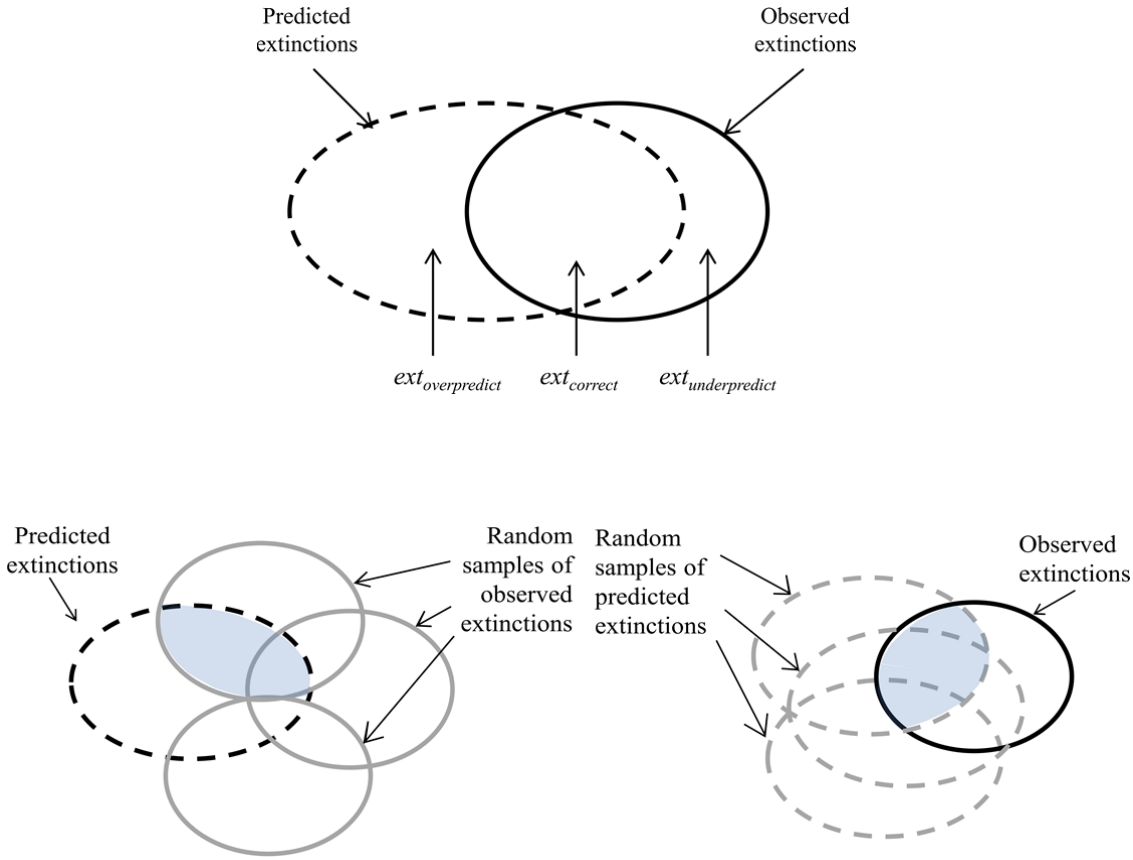

Figure B.1: Venn diagrams exemplifying measures of extinctions. The upper panel shows $ext_{overpredict}$ as number of species we predicted as extinct that were not extinct in the observations; $ext_{underpredict}$ as the number of extinct species we fail to predict; $ext_{correct}$ as the number of species we correctly predicted as extinct. $Ext_{correct}$ was calculated as is the sum of species we predicted to be extinct and the species that did not coexist and therefore were not included in the matrix of competition coefficients α_{ij}. On the lower panel, Venn diagrams exemplifying selections of random samples of observed extinctions (left panel) and predicted extinctions (right panel). Dashed lines are predictions, full lines are observations, black lines are real data (predicted from LV or observed), gray lines are random samples of LV predictions (dashed) and observation (full lines). For clarity reasons, only one overlapping region is highlighted. If $ext_{correct}$ is larger for the predicted ∩ observed intersection than for the random samples we conclude that the predictions were better than change predictions.

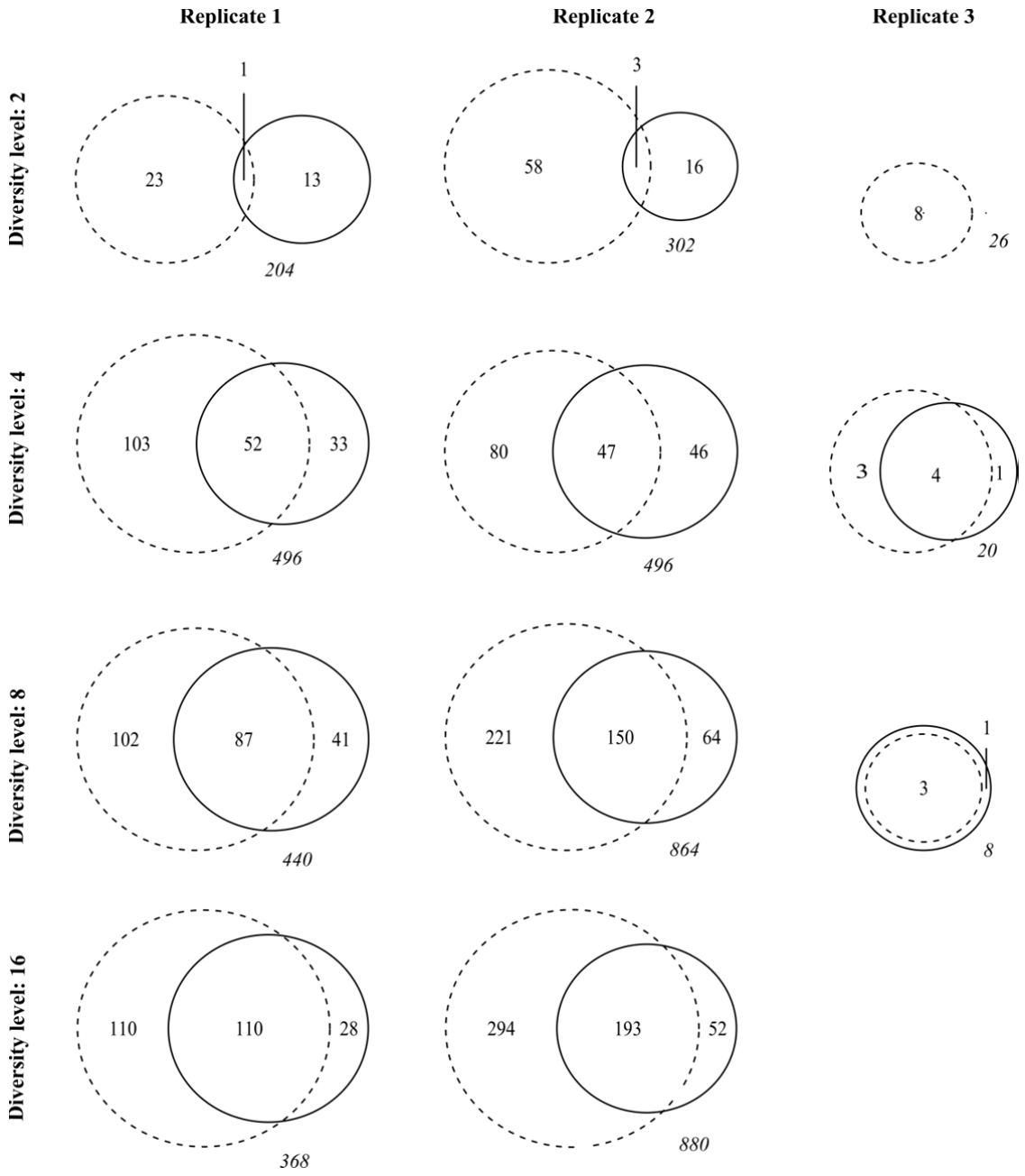

Figure B.2: Venn diagrams illustrating the total number of extinctions observed (full line) and predicted (dashed line) from each experimental replicate and for each diversity level. Numbers of observed extinctions differ among the three replicates because a different number of observed plots could be predicted. Numbers in italics are the maximum number of species which could go extinct, namely sown species richness × number of predicted community × number of years.

Appendix C

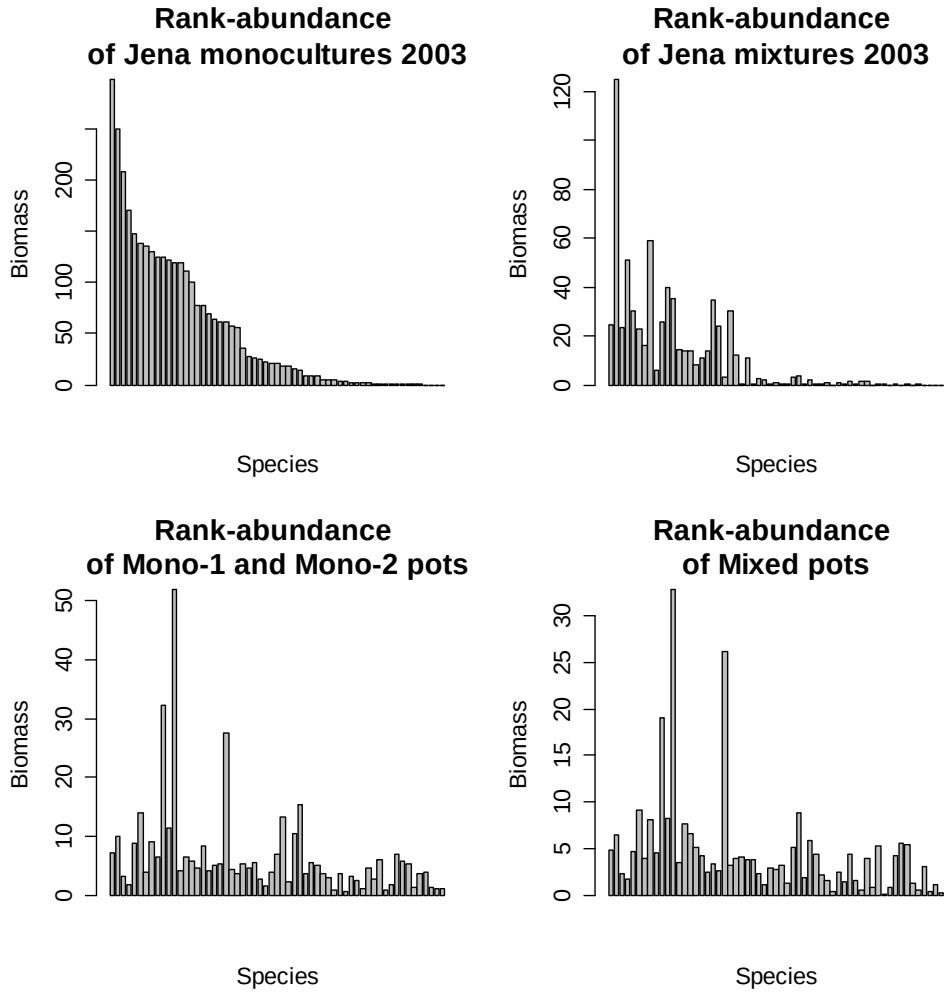

Figure C: Rank-abundance plots of species biomasses (g/m^2). The x-axis for all graphs was ordered following the species productivity in year 2003 in monocultures of the Jena Experiment (JE). Lower panels, were plotted using means over the three replicates of the PCE. Similar results were obtained plotting the values for the three replicates separately and these patterns were confirmed independently of which year of the JE was considered as reference (comparisons to other years are not shown).

Appendix D

Table D.1: Number of realized predictions from each replicates of the PCE, for diversity level and year. Total number of plots in the JE were: 16 monoculture plots from year 2003–2009, 15 for year 2010 and 14 for years 2011–2012; 16 plots of diversity level 2, 4 and 8 in all years and 14 plots of diversity level 16 for all years.

Rep	Diversity level	Year									
		2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
1	1	16	16	16	15	16	15	16	15	14	13
	2	10	10	10	11	10	10	10	11	10	10
	4	13	12	14	12	12	12	12	11	13	13
	8	6	7	6	5	5	3	4	7	6	6
	16	1	1	1	1	1	4	3	4	3	4
2	1	16	16	16	15	16	15	16	15	14	13
	2	16	15	15	15	15	15	15	15	15	15
	4	15	16	15	13	11	11	11	9	12	11
	8	13	15	14	14	10	7	8	10	9	8
	16	7	7	7	6	5	5	3	5	5	5
3	1	4	4	4	4	4	3	4	4	3	2
	2	2	1	2	1	1	2	1	1	1	1
	4	0	0	1	1	0	1	0	1	1	0
	8	0	0	0	0	0	0	0	0	0	1
	16	0	0	0	0	0	0	0	0	0	0

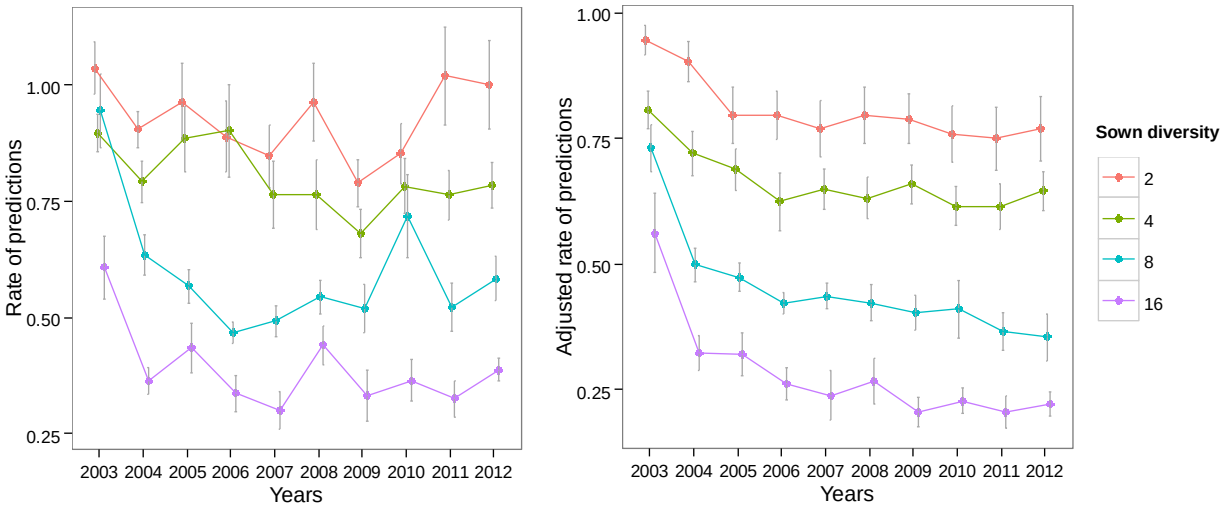

Figure D.2: Mean and standard errors of rate of predictions. In the left panel, rate of prediction is: predicted species richness / observed species richness; in the right panel adjusted rate of predictions is: number of species predicted and occurring / observed realized species richness. Values below 1 indicate that less species occurred in the predicted than in the observed communities. Results for monocultures were omitted as all monoculture had perfect predictions; i.e. single species never went extinct.

CHAPTER 3

Community reassembly after cessation of weeding in a biodiversity experiment

Enrica De Luca, Cameron Wagg, Alexandra Weigelt, Bernhard Schmid

Abstract

Despite the broad literature that investigates the biodiversity–ecosystem functioning relationship no consensus has yet been reached about the mechanisms behind community assembly. In particular, the transition from artificially to naturally assembled communities, often used to detect patterns of community reassembly, is expected to lead to species richness and community productivity convergences but not necessarily to convergence of species compositions.

Here, we compare artificially assembled communities and communities that undergo processes of natural reassembly. The data originate from the Jena Experiment, Germany, a biodiversity experiment established in 2002 with artificially assembled communities to simulate biodiversity loss. In 2009, the weeding treatment that maintained the sown diversity levels was interrupted in parts of the original plots, allowing for the natural reassembly of the communities.

We found that communities undergoing natural reassembly indeed experienced convergence of species richness and productivity, but we also found that species composition converged regardless of the sown species richness. Additionally, we found that complementarity effects were more positive and selection effects more negative in the reassembled communities than in the artificially maintained ones and that these effects became stronger over time.

Thus, our results show that communities undergoing natural reassembly tend to organize themselves in ways that reduce interspecific competition and that are independent of the initial species richness and composition.

Keywords: invasion, species richness, productivity, temporal variability, community convergence, additive partitioning

Introduction

Community assembly, namely how species abundances changes over time (Fukami and Morin 2003), is being investigated to uncover mechanisms behind the biodiversity–ecosystem functioning relationship. Common tools to study community assembly are experiments in which the transition from artificially to naturally assembled communities is allowed, often called invasion experiments (Pfisterer et al. 2004; Fukami et al. 2005; Bezemer and van der Putten 2007; Rixen et al. 2008; Roscher, Temperton, et al. 2009; Roscher et al. 2013).

Theory predicts that during such community reassembly the number of new species entering the community is higher in communities artificially assembled with lower sown species richness (e.g. Roscher et al. 2013) while extinctions instead are higher in communities artificially assembled with higher sown species richness (e.g. Pfisterer et al. 2004; Petermann et al. 2010). These opposite diversity-dependent mechanisms therefore lead to equilibrium of species richness (biogeographic theory, MacArthur and Wilson 1967; Pfisterer et al. 2004). In invasion experiments, the equilibrium of species richness is reached when the realized species richness of communities of different sown species richnesses become comparable among each other after allowing for natural assembly (Pfisterer et al. 2004; Rixen et al. 2008).

These changes in species richness in invasion experiments lead to the question of how different community properties might change during community reassembly. Studies show that some patterns described in biodiversity experiments with artificially assembled communities (Tilman 1996; Hector et al. 1999; Pfisterer and Schmid 2002) are also found in the naturally reassembled communities in invasion experiments (Pfisterer et al. 2004; Rixen et al. 2008; Roscher et al. 2013): the positive species richness–productivity relationship and the negative species richness–temporal variability of productivity relationship. Also, it was found that community composition does not appear to converge rapidly in invasion

experiments and rather that the communities are still distinct on the basis of their different sown species richness (Fukami et al. 2005; Roscher, Temperton, et al. 2009) or composition (Pfisterer et al. 2004; Fukami et al. 2005). This was explained by a convergence of species traits rather than species identity (Fukami et al. 2005; Roscher et al. 2014): while species identities do not appear to converge, species traits converge during community reassembly as the trait space available is determined by the environment while the species that will occupy the trait space is random within the species sharing similar trait-space. In a similar way, species phylogenetic similarity is also suggested as a driver of species assembly (Webb et al. 2002; Cadotte et al. 2008; Cavender-Bares et al. 2009; Allan et al. 2013). Species phylogeny was found to define the development of species abundance distributions with mechanisms promoting coexistence of distant relatives or mechanisms disadvantaging closely related species (Allan et al. 2013).

Whereas from previous studies we may deduct expected performances of communities undergoing natural reassembly, the mechanisms behind the reassembly itself have not yet been agreed upon. This is because processes which affect ecosystem functioning can have opposite effects on species assembly: the increase of productivity can in fact arise from increased dominance (positive selection effect) but also from increased evenness (positive complementarity effect) of the communities (Loreau and Hector 2001; Isbell et al. 2009). Different authors suggest that complementarity effects may increase over time so that the complementary interactions between species become more important in long-term experiments (Cardinale et al. 2007; Reich et al. 2012; Zuppinger-Dingley et al. 2014). However, to our knowledge, no study has yet applied additive partitioning (Loreau and Hector 2001) in an invasion experiment, probably because no monocultures of invasive species have normally been established.

Here we present a study where we used community and species aboveground biomass values from the Jena Experiment (Germany) to analyze community reassembly. In 78 plots

sown with 1, 2, 4, 8 or 16 species in 2002 we compared areas were we maintained sown richness levels by weeding from 2002 to 2013 (core areas) with adjacent areas where weeding was stopped in 2009 (invasion areas). Our hypotheses were the following: (1) species richness and productivity are higher in invasion areas than in core areas and temporal variation of productivity is lower in invasion areas than in core areas; (2) species richness and productivity in invasion areas converge; (3) final species composition in invasion areas remains distinct between plots with different initial species richness; (4) invasion leads to a stabilization of biomass production across years; (5) communities in invasion areas reorganize themselves in order to reduce competition, thus leading to an increase of complementarity effects and a decrease of selection effects.

As expected, we found that reassembled communities experienced an increase of aboveground biomass production, an increase of realized species richness and a decrease of temporal variability compared to the manipulated areas. Additionally, we observed an increase of complementarity and a decrease of selection effects in invasion areas compared to core areas, suggesting that communities did self-organize in order to avoid competition. Additionally, during the four years of natural reassembly, this pattern appeared to become stronger with time. However, we found that the final species composition of reassembled communities did not depend on the sown species richness and that instead species richness, community productivity and community composition of invasion areas converged over time independent of initial conditions.

Material and method

Experimental design

The Jena Experiment is located in the floodplain of the river Saale (Germany, 50°55’ N, 11°35’ E, 130 m altitude). The experiment was started in 2002 by establishing 78 plots of

different species compositions of 1–16 species from a pool of 60 grassland species that belong to four functional groups (grasses, short herbs, tall herbs and legumes, Roscher et al. 2004). The experiment was designed to simulate both a gradient of sown species richness (1, 2, 4, 8 and 16) and a gradient of sown functional group richness (1, 2, 3 and 4). The sown gradients were established and maintained by regular weeding. Each level of sown species richness was represented in 16 plots, with exception of species richness 16 (14 plots). The gradient of functional group richness levels was established with 34 plots containing species of a single functional group, 20 plots containing species of two functional groups, 12 plots containing species of three functional groups and 12 plots containing species of four functional groups. In autumn 2009 the original plot size of 20 × 20 m was divided into *core* area and *invasion* area. Each core area was kept regularly weeded whilst in each invasion area weeding was stopped, allowing for natural reassembly of the communities. Core areas measured 6 × 6 m and invasion areas measured 6 × 3 m.

In 2009 we established 3.5 × 3.5 m monoculture plots for each species belonging to the 60-species pool. These monocultures were established in 2009 together with a new experiment (Ebeling et al. 2014).

In 2011 we established 1.5 × 1.5 m monoculture plots for the following 31 species not belonging to the sown species pool but often colonizing the invasion areas (invasive species): *Bromus sterilis* L., *Capsella bursa pastoris* (L.) Med, *Cerastium holosteoides* Fries, *Cirsium arvense* (L.) Scop., *Convolvulus arvensis* L., *Conyza canadensis* (L.) Cronq., *Coronilla varia* L., *Echium vulgare* L., *Elymus repens* (L.) Gould, *Epilobium hirsutum* L., *Festuca arundinacea* Schreb., *Geranium pusillum* L., *Hypericum perforatum* L., *Lolium perenne* L., *Papaver rhoeas* L., *Poa annua* L.., *Poa compressa* L., *Potentilla reptans* L., *Rumex obtusifolius* L., *Silene dioica* (L.) Clairv., *Silene latifolia* Poir., *Silene vulgaris* (Moench) Garcke, *Solidago canadensis* L., *Sonchus asper* (L.) Hill, *Stellaria media* (L.) Vill., *Tanacetum vulgare* L., *Urtica dioica* L., *Veronica arvensis* L., *Veronica hederifolia* L.,

Veronica persica Poir., *Vicia sepium* L. These monocultures of new species were sown with a total density of 1000 viable seed per m^2 per plot. Seed numbers were adjusted according to germination rates from laboratory tests (Roscher et al. 2004). If a species did not germinate, we transplanted a maximum number of 20 adult individuals from the meadows in the nearest proximity of the Jena Experiment into a 1.5 × 1.5 m (see Appendix A). Following the typical mowing regimes for hay meadows, all established plots were mown twice per year, in early June and early September.

In the core area and in the invasion area of each plot we measured species aboveground biomass production and estimated species cover; both measures were taken two times per year, in spring and in summer. From 2009 onwards, plants in the core areas were harvested by cutting two randomly selected subplots of 0.2 × 0.5 m at 3 cm above ground level. Plants in the invasion areas were harvested by cutting one randomly selected subplot of 0.2 × 0.5 m at 3 cm above ground level. Monocultures of the species belonging to the 60-species pool were harvested first in summer 2012 and monocultures of invasive species were harvested first in spring 2012. Monocultures were harvest by cutting one randomly selected subplot of 0.2 × 0.5 m at 3 cm above ground level in the central 1 × 1 m of each plot. All plant material was sorted to species, dried at 70 C° for 48 hours and weighed. Aboveground species and community biomass per harvest was calculated as the average of the subplots sampled per plot. For further details, see Roscher et al. (2004).

Species cover was visually estimated in both core and invasion area on 3 × 3 m sampling quadrats in each plot following a decimal scale (Londo 1976): 1: ≤ 1%, 2: ≤ 5%, 10: 6–15%, 20: 16–25%, 30: 26–35%, 40: 36–45%, 50: 46–55%, 60: 56–65%, 70: 66–75%, 80: 76–85%, 90: 86–100%. Community cover was obtained by adding up species cover values; therefore community cover could exceed 100%. In this study we focused on the peak of aboveground productivity. We therefore only analyzed spring values of aboveground biomass production and cover measured in the period 2009–2013.

Data analysis

To quantify differences between core and invasion area in each plot we measured the following variables: realized species richness, total aboveground biomass and coefficient of variation (CV) of total biomass over the 5 years of observations; (Lehman and Tilman 2000; Bai et al. 2004). Realized species richness was derived from cover measures, the other variables were derived from aboveground biomass production. For mixed-species communities we calculated additive partitioning terms (Loreau and Hector 2001). To calculate complementarity (CE), selection (SE) and net biodiversity effects (NE) (Loreau and Hector 2001) we used monoculture biomass as a proxy of the yield of the species in monocultures. For the species belonging to the 60-species pool we used the spring harvest 2013 and for the new species colonizing the invasion areas we used the spring harvest 2012 as monocultures biomasses for the invasive species. We could not calculate additive partitioning for every invasion and every core areas because not all these monocultures yielded biomass or because some new species did not have monoculture plots. However, if in a mixture the total yield of the species with no biomass in monocultures was < 5% of the total community biomass, additive partitioning was calculated with the remaining species. The number of core areas out of a total of 78 plots for which we calculated additive partitioning in years 2003–2013 were 78, 77, 77, 77, 72, 74, 71, 70, 69, 67, 70. The number of invasion areas out of a total of 78 plots for which we calculated additive partitioning in years 2010–2013 were 67, 70, 70, 65. In the invasion area it was assumed that the colonizing species and the resident species had equal expected abundance, i.e. 1 divided by species richness, to calculate CE and SE.

Differences in realized species richness, total aboveground biomass and CV of total aboveground biomass between core and invasion area were evaluated with mixed-effects general linear models carried out with GenStat (15th Edition) using the residual (=restricted) maximum likelihood method and analysis of variance (ANOVA) type of output. Additive

partitioning terms were computed with the software R, v3.0.2 (R Development Core Team, http://www.R-project.org).

To detect similarity in community composition we used the Jaccard dissimilarity index (Greig-Smith 1983). This metric allows to compare the species composition of two communities and ranges from 0 (same species in two communities) to 1 (maximum dissimilarity, no common species between the two communities). We measured the Jaccard dissimilarity index for the two following types of community pairs: i) pairwise comparison of all invasion areas harvested in the period 2009–2013 and ii) pairwise comparison of each plot in two adjacent years. Additionally, to measure similarity in community composition between all invasion areas in year 2009 and in year 2013, we performed Nonmetric Multidimensional Scaling (NMDS). NMDS attributes a spatial positon to communities on the basis of their species composition and it is commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin 1987). NMDS is a method that standardizes the scaling in the result and adds species scores to the site ordination whilst attempting to find a stable position in the bi-dimensional space via several random trials. We used 100 random trials and the Jaccard distance method to define the position of each community in the NMDS bi-dimensional plane. Both Jaccard dissimilarity and NMDS were computed with the software R, v3.0.2 (R Development Core Team, http://www.R-project.org).

Results

Areas where natural reassembly of the communities was allowed (invasion areas) were more productive, more species-rich and less variable in productivity (CV) than areas where the sown diversity was maintained by weeding (core areas). Species richness and community productivity converged across plots of different sown species richness. Community compositions in invasion areas also converged over time regardless of the level of sown

species richness. Finally, we observed an increase in CE and a decrease in SE in invasion areas compared to core areas and a strengthening of these patterns over the four consecutive years 2010–2013.

Community assembly: realized diversity and species composition

As expected, the cessation of weeding led to an increase of realized species richness in the invasion areas (Fig. 1a). The increase of realized species richness was observed at each sown richness level 1–16 and it was visible immediately after the cessation of weeding in 2010 (Fig. 1a). The increase reached a maximum in 2012 as indicated by the significant quadratic term in the statistical model (Table 1: *year_linear*, $F_{1,249.3} = 208$, $P < 0.001$; *year_quadratic*, $F_{1,249.2} = 68.78$, $P < 0.001$). However, the largest increases of realized species richness were observed comparing year 2009 and all other years (Table 1: *year_2009*, $F_{1,292.6} = 1357$, $P < 0.001$). Additionally, we found that communities of different sown richness levels showed different realized richness levels only in year 2009, namely, before allowing for natural reassembly (Table 1: *year_2009.sowndiv,* $F_{1,79.1} = 56.47$, $P < 0.001$). Thus, from 2010 onwards, the realized species richness in the invasion areas was not different among the different levels of sown species richness (Fig. 1a and Table 1).

The cessation of weeding and subsequent invasion did not cause sown species to go extinct, as the number of sown species remained approximately the same in core areas and in invasion areas (Fig. 1a). However, total cover of sown species decreased in the communities of lower sown richness (Fig. 1b, sown species richness 1 and 2). The increased realized species richness in the invasion areas was mainly due to the invasion by species belonging to the initial 60-species pool (Fig. 1a) while invasion by new species occurred less frequently (Fig. 1a).

We found that the increase of realized species richness in the invasion areas led to increased similarity of community compositions. The community compositions of all 78

communities prior to invasion (year 2009) were highly dissimilar (mean dissimilarity calculated as Jaccard dissimilarity across all plots in year 2009 was 0.95). As soon as weeding was stopped and natural reassembly of the communities was allowed, communities became more similar (0.67 mean dissimilarity across all invasion areas in year 2010) and appeared to reach a plateau from year 2012 onwards (mean dissimilarity across all invasion areas in year 2011, 2012 and 2013 was 0.62, 0.57 and 0.58, respectively). This convergence of community compositions (Fig. 2) was independent from the initial species richness (Fig. 2a) and initial functional group richness (Fig. 2b).

The species turnover in the invasion areas stabilized across years, but until 2012 remained higher in plots with lower rather than higher levels of sown species richness (Fig. 3). The largest variations among all years were observed between years 2009 and 2010, thus due to the species invading the communities. Between 2012–2013 species turnover did not differ anymore between invasion areas of different initial species richness (Fig. 3).

Community productivity: biomass production and additive partitioning

Aboveground biomass production was always higher in invasion areas than in core areas at each level of sown species richness and in each year (Fig. 4a). The mean biomass production in core vs invasion areas for each sown richness level in year 2013 was: 84 vs. 423 g/m^2, 168 vs. 374 g/m^2, 170 vs. 391 g/m^2, 188 vs. 371 g/m^2 and 271 vs. 407 g/m^2 in 1-, 2-, 4-, 8- and 16-species communities, respectively. Total productivity in the invasion areas was not dependent on the sown richness, while species richness in the core areas positively affected productivity (Table 2: *INV.sowndiv*, $F_{1,70.01} = 11.5$, $P = 0.001$) according to the classic biodiversity–productivity relationship already largely described in the Jena Experiment. The differences in productivity between core and invasion area increased with time (Fig. 4a and Table A2: *INV.year_linear*, $F_{1,310.6} = 6.68$, $P = 0.01$).

Among all functional groups, only the presence vs. absence of legumes among the sown species affected the increased biomass production after invasion: the differences in biomass production between core and invasion area were higher for communities with no sown legumes (Fig. 4b and Table 2: *INV.sown_leg*, $F_{1,69.5} = 15.04$, $P < 0.001$). Additionally, even though a larger portion of variability was explained by the contrast with year 2009 (Table 2: *INV.year_2009.sown_leg*, $F_{2,310.3} = 21.44$, $P < 0.001$), the increased biomass production in communities where no legumes were sown, became stronger with time (Fig. 4b and Table 2: *INV.year_linear.sown_leg*, $F_{2,309.5} = 3.02$, $P = 0.05$).

We also investigated the role of sown functional group richness and found that, similar to sown species richness, larger sown functional group richness led to smaller divergence between core and invasion area (observed values in year 2013 in core and invasion areas: 1-functional groups: 128 vs. 419 g/m^2; 2-functional groups: 185 vs. 354 g/m^2; 3-functional groups: 232 vs. 400 g/m^2; 4-functional groups: 234 vs. 377 g/m^2). However, the effect of sown functional group richness was only marginal: the role of legumes and sown species richness was much larger than the effect of sown functional group richness (Table 2). We did not find any temporal patterns of functional group richness.

In order to disentangle a potential legacy effect of the sown community on the realized community, we also quantified the role of realized species richness in shaping community assemblage. We focused on species richness and on legumes because, on one hand, the effect of sown functional group richness was marginal compared to sown species richness and to the presence of sown legumes and, on the other hand, all functional groups appeared in each invasion area. We found that areas with high realized species richness also had high productivity (Table 3: *obsdiv*, $F_{1,581.6} = 162.9$, $P < 0.001$), and that this positive biodiversity effect was not different between core and invasion areas (Table 3: *INV.obsdiv*, $F_{1,457.2} = 0.66$, n.s.). If we added the effect of realized species richness, the sown species richness in the invasion areas was not related to community productivity while in the core

areas it corresponded to an increase of productivity (Table 3: *INV.sowndiv*, $F_{1,563.1} = 4.31$, $P = 0.038$). Also, the observed pattern was constant across time (Table 3: *INV.year_linear.obsdiv*, $F_{2,465,1} = 0.11$, n.s. and *INV.year_linear.sowndiv*, $F_{2,387.8} = 1.22$, n.s.). The realized proportion of legumes present in a community positively influenced community productivity (Table 3: *obs_leg_prop*, $F_{1,556.6} = 29.59$, $P < 0.001$) and this positive effect of legumes was higher in the invasion than in the core areas (Table 3: *INV.obs_leg_prop*, $F_{1,483.8} = 10.24$, $P = 0.001$). Additionally, the positive effect of legumes on community productivity increased over time (Table 3: *INV.year_linear.obs_leg_prop*, $F_{2,503.9} = 4.93$, $P = 0.008$).

In the analysis of the CV of productivity calculated for the period 2009–2013 we found that core areas were more variable than invasion areas (mean CV across all communities 0.47 for core and 0.34 for invasion areas). Invasion areas of higher sown richness showed the same variability as their corresponding core areas while invasion areas of lower sown richness were more stable than their corresponding core areas (Fig. 5; Table 4: *INV.sowndiv*, $F_{1,72} = 3.58$, $P = 0.062$). Sown functional group richness positively affected stability of productivity (Table 4: *funcgr*, $F_{1,72} = 7.16$, $P = 0.009$), and this positive effect was observed both in core and invasion areas (Table 4: *funcgr.INV*, $F_{1,72} = 1.81$, n.s.). Among all functional groups the one that had the strongest influence on the CV of productivity when sown in the community was the group of short herbs (*SH*). Their presence among the sown species reduced the CV in core areas and increased it in invasion areas (Fig. 5b; Table 4: *INV.SH*, $F_{1,72} = 7.74$, $P = 0.007$).

In order to quantify the relative contribution of complementarity effect (CE) and selection effect (SE), we applied additive partitioning (Loreau and Hector 2001) to the aboveground biomass measured for communities in core and invasion areas. We found that cessation of weeding caused an increase of CE and a decrease of SE in invasion areas over time (Fig. 6). In the core areas both CE and SE stabilized at lower levels around zero.

Discussion

We showed that communities undergoing natural reassembly after cessation of weeding were more diverse, more productive and more stable in their productivity than communities where the sown richness was artificially maintained by weeding. Additionally, as found in earlier studies (Pfisterer et al. 2004; Fukami et al. 2005; Rixen et al. 2008; Roscher, Temperton, et al. 2009), the natural reassembly following the cessation of weeding led to a rapid convergence of realized species richness and productivity among plots of different sown species richness; species composition also converged, but more slowly. The transition from weeded to reassembled communities was dominated by mechanisms leading to increased stability (negative SE) and decreased interspecific competition (increased CE).

Effects of community reassembly on species diversity and composition

We found that allowing previously weeded communities to reassemble led to an increase of species richness in every community and to a similar realized richness across reassembled communities, regardless of the sown richness of the weeded communities. The increase of species richness was visible immediately in the first year after cessation of weeding (year 2010), soon reached a maximum and then often declined slightly, indicating a slight overshooting (see Fig. 1). The increases of species richness across all invasion areas were primarily due to an increase in the number of species that belonged to the initial 60-species pool at the experimental site. Interestingly, we observed almost no extinctions of sown species during reassembly, but only a decrease of their abundance, especially in plots of low sown richness (see Fig. 1).

Previous studies about community reassembly found that invasion easily increases species richness (Bezemer and van der Putten 2007; Roscher, Beßler, et al. 2009; Roscher, Schmid, et al. 2009), resulting in equal species richness across communities of originally different sown richness (Pfisterer et al. 2004; Rixen et al. 2008). However, in the latter two

studies the invasion of new species caused extinctions of originally sown species which was not the case in Roscher et al. (2013).This discrepancy might be due to a longer duration of the weeding phase in Roscher et al. (2013) and the present study. Therefore species with lower competitive ability or species for which the biotope space was narrow had left the community before cessation of the weeding.

In our experiment, the increase of species richness during community reassembly led to convergence of species composition. Previous studies that attempted to identify the changes in community compositions following invasion, both in other experimental setups (Pfisterer et al. 2004; Fukami et al. 2005), or in the Jena Experiment (Roscher, Temperton, et al. 2009), are partially contradicting our new finding. We observed increasing similarity across communities and we found that both originally sown species richness and sown functional group richness had no role in defining the final species composition in the invasion areas (see Fig. 2). Also, in the invasion areas, the species turnover between years was limited (see Fig. 3): community composition in invasion areas, after an initial change stabilized regardless of the sown species richness. Thus, our findings suggest that sown species richness might have only limited impacts on the characteristics of the community that undergo reassembly. The divergence between our findings and the findings of previous studies could have different reasons. First, our experiment was characterized by reassembly of communities after cessation of weeding that had been carried out for several years whereas some of the previous studies compared weeded and un-weeded plots from the time of the initial establishment of the communities (Fukami et al. 2005; Bezemer and van der Putten 2007; Roscher, Temperton, et al. 2009; Roscher et al. 2013). Furthermore, colonization of existent communities is dependent on both the resident community and on the characteristics of the invasive species (Milbau et al. 2005; Emery 2007; Roscher, Beßler, et al. 2009). The patterns observed at the community level do not necessarily need to be relevant for invasion resistance (Roscher, Beßler, et al. 2009). Thus, it is not necessarily surprising that

characteristics of the sown communities are not responsible for post-weeding assembly processes and instead it could be that in our experiment the role of the invasive species overcame the role of the sown species. This might be dependent on mechanisms related to functional trait similarity (Fukami et al. 2005; Roscher et al. 2014) or phylogenetic similarity (Cadotte et al. 2008; Allan et al. 2013) among resident species or among invasive species and resident species. In this study we did not account for these aspects.

Effects of community reassembly on community productivity and stability of productivity

After reassembly, invasion areas increased productivity and decreased temporal variability. The increase of productivity was positively related to the realized species richness and the realized richness–productivity relationship was identical between core and invasion areas. Differences in productivity between invasion and core areas increased with time; however, the largest change in productivity in the invasion areas was immediately after cessation of weeding (year 2010). All invasion areas reached similar mean productivity; and sown species richness did not affect the productivity of the communities after reassembly.

Previous studies also have described an increase of productivity and of temporal stability after community reassembly which led to a convergence of productivity (Pfisterer et al. 2004; Fukami et al. 2005; Roscher, Temperton, et al. 2009). We observed an increase of productivity as a consequence of the increase of species richness, in line with a large literature body that shows positive biodiversity–productivity relationships (Reich et al. 2012). However, lower productivity in invaded communities compared to sown communities was also sometimes observed (Bezemer and van der Putten 2007). Such contrasting results may be due to differences between the experimental design (note that the study of Bezemer and van der Putten (2007) differs from ours also in terms of convergence of richness, community composition and temporal stability). As previously mentioned, some invasion experiments in

fact compared artificially maintained communities and communities which assembled from scratch by sowing (Fukami et al. 2005; Bezemer and van der Putten 2007; Roscher, Temperton, et al. 2009; Roscher et al. 2013). Thus, results of these studies include successional mechanisms of community assembly which do not pertain to our experiment, where instead reassembly took place on plots that had already assembled communities.

We found that the presence of legumes in the sown communities affected productivity differentially in invasion and in core areas: the differences in productivity between invasion and core areas were larger in communities where no legumes were sown (see Fig. 3b, right panel). However, the realized proportion of legumes in the community was a stronger driver of the differences in productivity between core and invasion areas than was the presence of legumes among the sown species (see Table 3). This is in line with our previously described findings where we discussed how in invasion areas the realized species richness was a better driver of the increase of productivity than was the sown species richness. Additionally, a number of studies have shown that N_2-fixing legume species positively interact with other species, contributing to overyielding with increasing species richness (Mulder et al. 2002; Cardinale et al. 2007; Roscher et al. 2008; Bessler et al. 2009; Marquard et al. 2009), and similar patterns were observed also in invasion experiments (Bezemer and van der Putten 2007; Roscher, Beßler, et al. 2009).

We also investigated the effects of functional group richness on community productivity and found that higher sown functional group richness led to smaller productivity divergence between core and invasion areas than did lower sown functional group richness. However, we also found that the effect of sown functional group richness was of less importance than the effect of sown species richness. The effect of functional group richness is confounded within the effect of sown species richness, however less by design in the Jena Experiment than in other experiments (Le Roux et al. 2013).

In terms of temporal stability of productivity, we found that invasion areas were more stable than core areas and that the temporal stability of productivity was related to sown species richness. However, communities with high sown species richness were equally stable in invasion and in core areas, indicating that a higher species richness was more important than a more natural species composition for stable productivity. All invasion areas reached comparable levels of stability, due to their convergence of species richness and productivity. Nevertheless, stability of productivity was also related to species turnover, which also became more stable in the years (see Fig. 3). These findings are in accordance with the insurance hypothesis of biodiversity (Yachi and Loreau 1999): the presence of more species will buffer variations at the community level as different species across time will respond differently to competition, environmental variation and demographic stochasticity. We found additionally that among all functional groups, the presence of short herbs (SH) was affecting temporal stability of productivity: plots without sown SH increased their stability during invasion more strongly than plots with sown SH (see Fig. 5b). Invasion areas with sown SH were actually less stable than those without sown SH. Possibly, this is related to the trait space used by all or some SH species. Species of the SH group might have a high degree of similarity in their niche space and therefore, interspecific competitions among species belonging to the same group would lead to instability of productivity. Observation in the field supported this hypothesis because the most common SH species had similar growth form (basal tuft), potentially leading to high interspecific competition. However, this interpretation of our results would need to be confirmed and supported with analysis of trait data.

Finally, we investigated mechanisms of community reassembly by additive partitioning of biodiversity effects and found that complementarity effects (CE) increased and selection effects (SE) decreased during reassembly. A number of studies partitioned biodiversity effects on productivity and found that over time CE generally increases (Hector et al. 2010; Reich et al. 2012; Zuppinger-Dingley et al. 2014). The increased CE over time

can be explained as increasing functional diversity and/or replacement of functionally similar species (Reich et al. 2012) or genotypes (Zuppinger-Dingley et al. 2014) by functionally dissimilar ones. Simultaneously, the decrease of SE suggests the presence of stabilizing forces on community productivity (Loreau and Hector 2001). Thus, species in the invasion areas of the Jena Experiment, due to the optimization of the use of the niche space and to the increase of temporal stability of productivity, assembled in order to reduce the competition among the co-occurring species in the communities.

In summary, we found that (1) species richness and productivity were higher in invasion areas than in core areas and that (2) species richness and productivity in invasion areas converged. (3) The final composition in invasion areas had converged regardless of sown species richnesses. (4) Invasion led to increased temporal stability of productivity and (5) the mechanism behind community reassembly led to a reduction of competition. Our findings suggest that community reassembly after cessation of weeding does not depend on sown community characteristics and instead community composition of invasion areas converges regardless of initial species richness, thus reaching similar species richness and productivity.

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Tables

Table 1: Anova table from REML; response variable: *observed species richness in invasion areas from 2009–2013*. Observed species richness in year 2009 corresponds to observed species richness in core areas. Terms: *y*ear_*2009*, contrast for year 2009; *y*ear_*linear*, year linear; *y*ear_*quadratic*, year quadratic (*y*ear_*linear* × *y*ear_*linear*); *sowndiv*, logarithm of sown species richness; *PL* (random term), community identification at the plot level.

Fixed term	**Wald statistic**	**F statistic**	**d.d.f.**	**F pr**
year_2009	1356.99	1356.99	292.6	<0.001
year_linear	208.00	208.00	249.3	<0.001
year_quadratic	68.78	68.78	249.2	<0.001
sowndiv	19.73	19.73	75.0	<0.001
year_2009 * sowndiv	56.47	56.47	79.1	<0.001
Random terms				
PL, year_linear * PL, year_quadratic * PL (negative variance component)				

Table 2: Anova table from REML; response variable: *total biomass from 2009–2013*. This analysis focuses on the role of the sown species in driving community productivity. Terms description*: INV,* invasion vs main areas; *y*ear*_2009,* contrast for year 2009; *y*ear*_linear*, year linear; *YR,* year factorial; *sown_leg,* presence-absence of sown legumes; *funcgr,* sown functional group richness; *sowndiv*, logarithm of sown species richness; PL (random term), community identification at the plot level.

Fixed term	**Wald statistic**	**F statistic**	**d.d.f.**	**F pr**
INV	273.48	273.48	69.9	<0.001
year_2009	7.6	7.6	311.9	0.006
year_linear	43.18	43.18	309.7	<0.001
YR	2.79	1.39	406	0.25
sown_leg	34.31	34.31	71.9	<0.001
funcgr	1.3	1.3	71.5	0.258
sowndiv	32.16	32.16	72.6	<0.001
INV * year_2009	63.72	63.72	313	<0.001
INV * year_linear	6.68	6.68	310.6	0.01
INV * YR	11.28	5.64	406.1	0.004
INV * sown_leg	15.04	15.04	69.5	<0.001
INV * funcgr	7.85	7.85	69.3	0.007
INV * sowndiv	11.5	11.5	70.1	0.001
INV * year_2009 * sown_leg	42.89	21.44	310.3	<0.001
INV * year_2009 * funcgr	2.51	1.26	309	0.286
INV * year_2009 * sowndiv	10.06	5.03	313.3	0.007
INV * year_linear * sown_leg	6.05	3.02	309.5	0.05
INV * year_linear * funcgr	1.9	0.95	309.1	0.388
INV * year_linear * sowndiv	2.39	1.19	310.5	0.305
Random terms				
PL, PL * INV (negative variance component), PL * INV * year_2009 and PL * INV * year_linear				

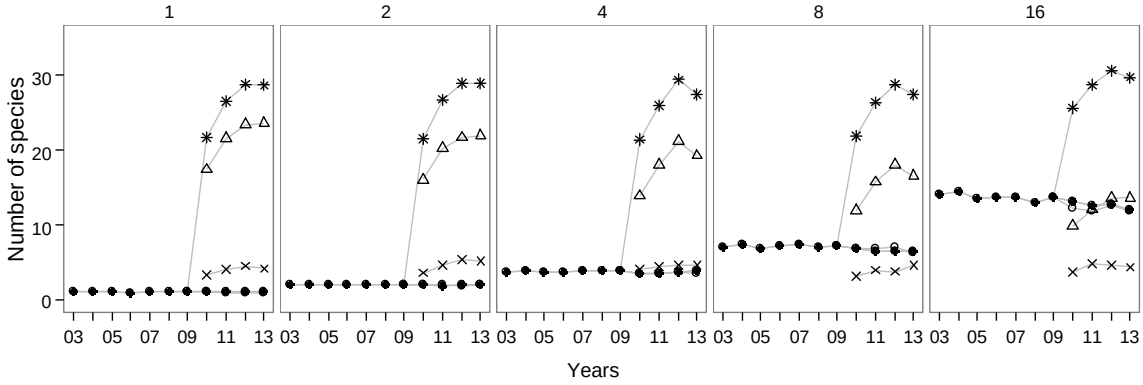
Table 3: Anova table from REML; response variable: *total biomass from 2009–2013*. This analysis focuses on the comparison of the role of the species sown and species occurring in the community in driving community productivity. In this final model we omitted the interactions with sown functional group richness to focus on species richness and on presence-absence of legumes. Terms description*: INV,* invasion vs main areas; *year_2009,* contrast for year 2009; *year_linear*, year linear; *YR,* year factorial; *obs_leg_prop,* observed proportion of legumes; *sown_leg_prop* sown proportion of legumes; *obsdiv*, logarithm of realized species richness; *sowndiv*, logarithm of sown species richness; *PL* (random term), community identification at the plot level.

Fixed term	**Wald statistic**	**F statistic**	**d.d.f.**	**F pr**
INV	271.82	271.82	183.4	<0.001
year2009	7.45	7.45	342.9	0.007
year_linear	44.27	44.27	353.6	<0.001
YR	2.89	1.44	426.3	0.237
obs_leg_prop	29.59	29.59	556.6	<0.001
sown_leg_prop	2.05	2.05	126.5	0.154
obsdiv	162.9	162.9	581.6	<0.001
sowndiv	1.83	1.83	131.5	0.178
INV * year_2009	1.64	1.64	355.5	0.201
INV * year_linear	4.3	4.3	374.2	0.039
INV * YR	14.07	7.03	430.4	<0.001
INV * obs_leg_prop	10.24	10.24	483.8	0.001
INV * sown_leg_prop	0.04	0.04	233.6	0.846
INV * obsdiv	0.66	0.66	457.2	0.416
INV * sowndiv	4.31	4.31	563.1	0.038
INV * year_2009 * obs_leg_prop	12.22	6.11	658.4	0.002
INV * year_2009 * sown_leg_prop	6.95	3.47	575.1	0.032
INV * year_2009 * obsdiv	1.42	0.71	556.5	0.492
INV * year_2009 * sowndiv	0.73	0.36	532.5	0.695
INV * year_linear * obs_leg_prop	9.86	4.93	503.9	0.008
INV * year_linear * sown_leg_prop	7.34	3.67	338	0.026
INV * year_linear * obsdiv	0.22	0.11	465.1	0.898
INV * year_linear * sowndiv	2.43	1.22	387.8	0.297
Random terms				
PL, PL * INV (negative variance component), PL * INV * year_2009 and PL * INV * year_linear				

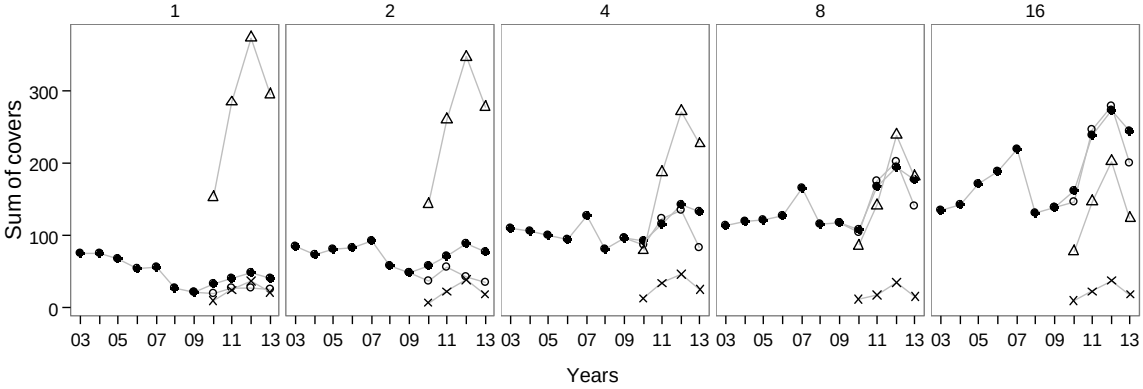
Table 4: Anova table from REML; response variable: *coefficient of variation (CV)*. CV was calculated across the period 2009–2013, thus no temporal terms are included. Terms description*: INV,* invasion vs main areas; *SH,* presence-absence of sown short herbs; *funcgr,* sown functional group richness; *sowndiv*, logarithm of sown species richness; *PL* (random term), community identification at the plot level.

Fixed term	**Wald statistic**	**F statistic**	**d.d.f.**	**F pr**
INV	17.62	17.62	72.0	<0.001
SH	0.76	0.76	72.0	0.387
funcgr	7.16	7.16	72.0	0.009
sowndiv	17.97	17.97	72.0	<0.001
INV * SH	7.74	7.74	72.0	0.007
INV * funcgr	1.81	1.81	72.0	0.182
INV * sowndiv	3.58	3.58	72.0	0.062
Random terms				
PL (negative variance component)				

Figures

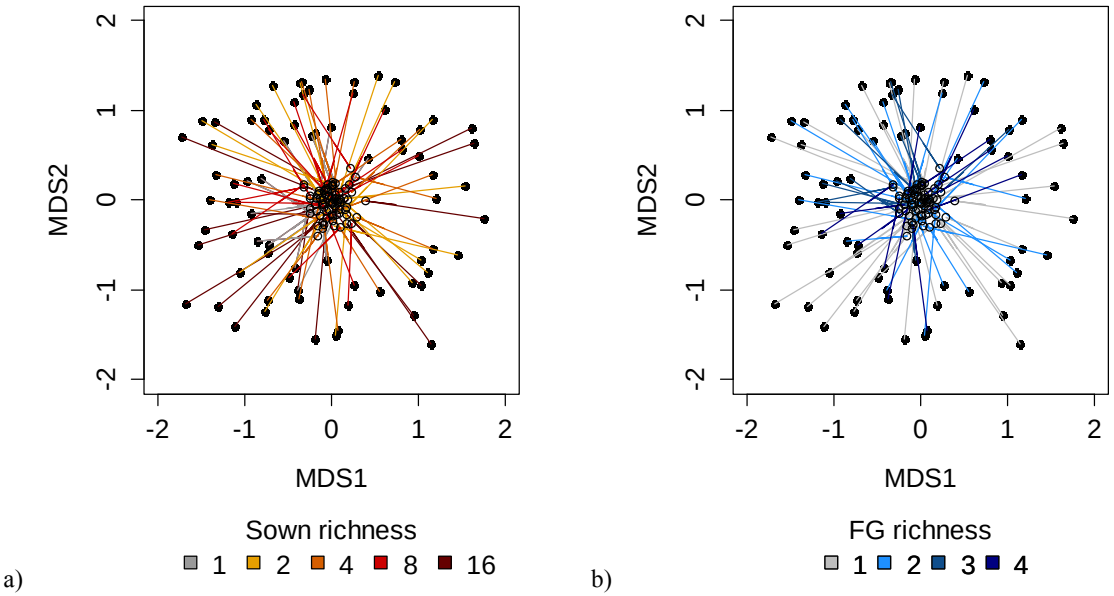


a)



b)

Figure 8: Plots of realized species richness over time in core areas and invasion areas for sown richness levels as: a) mean number of species in the upper panels, and b) mean of sum of cover values in the lower panels. Each symbol represents a different component of the realized species richness: ● – sown species in the core area; ○ – sown species in the invasion area; ▵ – invasive species belonging to the sixty species pool in the invasion area; × – invasive species not belonging to the sixty species pool in the invasion area; * – total number of observed species in the invasion area.



a) b)

Figure 2: Positions in 2009 ● and in 2013 ○ of the invasion areas in the two-dimensional space defined by the first two components of Nonmetric Multidimensional Scaling (NMDS). Lines connect same communities before and after allowing for natural reassembly. The different colors of the lines refer to a) the different sown species richness of the communities, b) the different sown functional group richness of the communities.

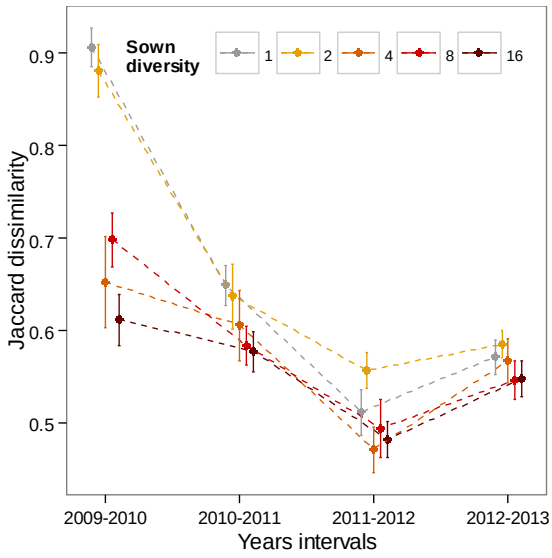


Figure 3: Mean and standard error of Jaccard dissimilarity index in the invasion areas over time. Jaccard dissimilarity was calculated for each plot as the comparison of community compositions in years *n* and *n+1*. Different colors represents different levels of sown species richness.

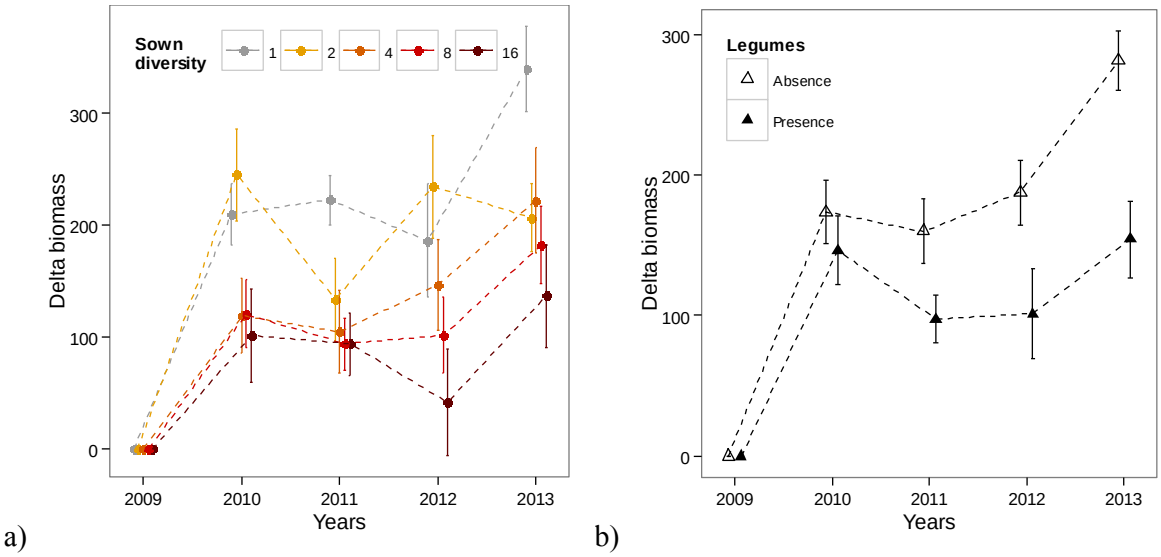


Figure 4: Changes of delta biomass over time shown a) for the different levels of sown species richness and b) for presence or absence of legumes among the sown species. Delta biomass is calculated in each plot as biomass in the invasion area – biomass in the core area. Thus, values above 0 indicate increased of biomass production in the invasion area compared to the core area. Measures in 2009 are the same for invasion areas and for core areas since the natural reassembly was measured first in year 2010.

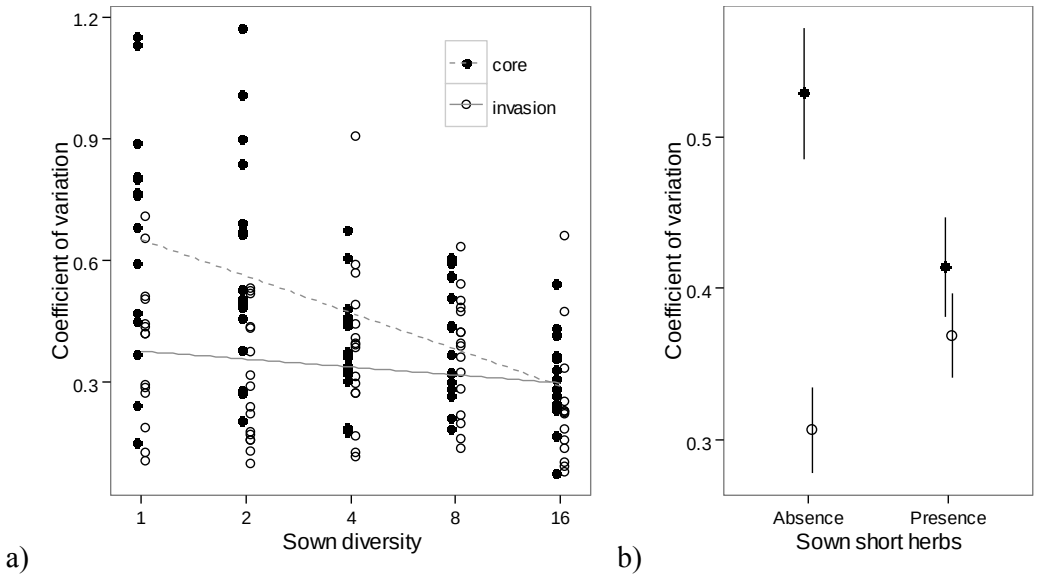


Figure 5: Coefficient of variation (CV) of core areas and of invasion areas in the period 2009–2013. In a) each point represents a CV value calculated over five harvests (2009–2013); two regression lines show CV–sown species richness relationship in core and in invasion areas. In b) mean and standard error of CV in core and in invasion areas in the presence or in the absence of short herbs in the sown communities.

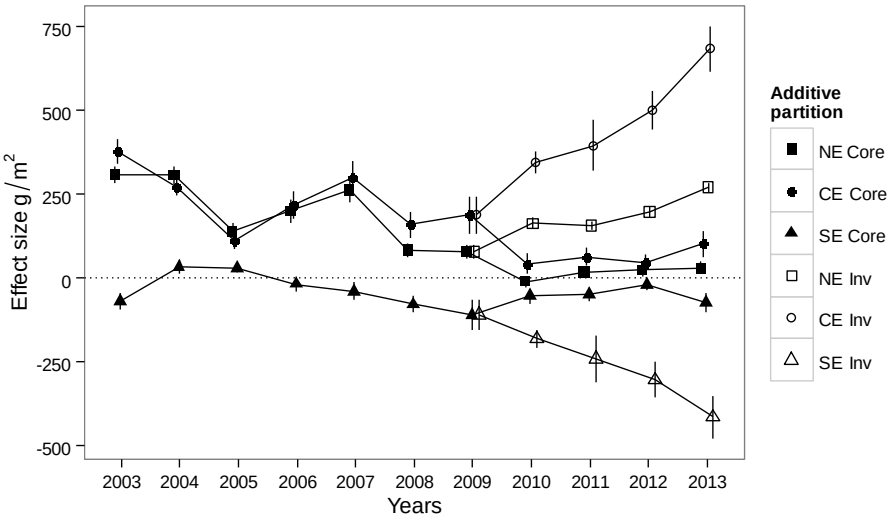


Figure 6: Mean and standard error of additive partitioning terms (net effect, *NE*; complementarity effect, *CE*; selection effect, *SE*) from aboveground biomass measured in core areas in years 2003–2013 and in invasion areas in year 2010–2013.

Appendix A

Table A: Procedure or the result of the procedure in the establishment of the monocultures of invasive species. In case of poor germination of the species, we transplanted a maximum number of 20 individuals into the central 1 × 1 m of the monocultures area. The number of individuals transplanted was proportional to the availability of the species in the meadows around the Jena experiment.

Species	**Procedure**
Bromus sterilis:	grown
Capsella bursa pastoris:	grown and 20 individuals transplanted
Cerastium holosteoides:	1 individual grown and 20 individuals transplanted
Cirsium arvense:	1 individual grown and 20 individuals transplanted
Convolvulus arvensis:	not germinated, 10 individuals transplanted
Conyza canadensis:	not germinated, 10 individuals transplanted
Coronilla varia:	grown
Echium vulgare:	not germinated, no transplanted material
Elytrigia repens:	grown
Epilobium hirsutum:	not germinated, 5 individuals transplanted
Festuca arundinacea:	grown
Geranium pusillum:	not germinated, no transplanted material
Hypericum perforatum:	not germinated, 5 individuals transplanted
Lolium perenne:	grown
Papaver rhoeas:	10 individual grown, 5 individuals transplanted
Poa annua:	grown
Poa compressa:	not germinated, no transplanted material
Potentilla reptans:	not germinated, 20 individuals transplanted
Rumex obtusifolius:	not germinated, 2 individuals transplanted
Silene dioica	not germinated, no transplanted material
Silene latifolia:	grown
Silene vulgaris:	grown
Solidago canadensis:	not germinated, 20 individuals transplanted
Sonchus asper:	grown
Stellaria media:	5 individuals grown, 5 individuals transplanted
Tanacetum vulgare:	not germinated, 20 individuals transplanted
Urtica dioica:	not germinated, 20 individuals transplanted
Veronica arvensis:	not germinated, 5 transplanted material
Veronica hederifolia:	not germinated, no transplanted material
Veronica persica:	grown
Vicia sepium:	grown

GENERAL DISCUSSION

The rise in the human-induced loss of biodiversity over the past century has pressed the scientific community to focus on the role that biodiversity plays in ecosystem functioning. Although previous work demonstrated the positive effect of biodiversity on some ecosystem functions such as productivity, stability of productivity and species assembly, the underlying mechanisms have not yet been fully unrevealed. In this thesis I investigated mechanisms underpinning biodiversity–ecosystem functioning relationships in manipulated grassland communities. Firstly, I found that species richness promotes community productivity (chapter 1 and chapter 3) and temporal stability of community productivity (chapter 1). Increased temporal stability of productivity in more species-rich communities was largely but not uniquely driven by asynchronous biomass fluctuation at the species level (chapter 1). Additionally, I found that interspecific species competition is particularly crucial in the phases of the establishment of a community (chapter 2) and that communities organize themselves in order to reduce interspecific competition (chapter 3). The detailed discussion of these results is provided at the end of each chapter. Here I synthesize the concepts of the ecological community addressed in each chapter in order to build a broader picture of how my research connects aspects of community stability, competitive interactions and community assembly and to provide insights into future research.

Effects of biodiversity loss with a the focus on stability

In summary, this thesis shows how species richness in the Jena Experiment promotes the most commonly analyzed ecosystem functions: community productivity (chapter 1 and chapter 3) and temporal stability in community productivity (chapter 3). My results were in line with previous studies both of the Jena Experiment (Marquard et al. 2009; Roscher et al. 2011) and of other biodiversity experiments (Tilman 1996; Yachi and Loreau 1999; Hector et al. 2010).

In the last decades, the scientific community has progressively shifted its interest from ecosystem functions to the stability of these functions (Tilman 1996; Hector et al. 2010). The topic of stability and in particular the stability of the most commonly used proxy of ecosystem functioning, productivity, is of importance in the context of climate change (Tilman and Downing 1994; Loreau et al. 2001). Under natural conditions ecosystems are exposed to fluctuating biotic and abiotic environments that have been predicted to become more extreme or more variable in time. Consequently, these fluctuations affect and alter ecosystem dynamics and functioning (Cardinale et al. 2012). Because human activities perpetrate both biotic and abiotic changes, understanding how the stability an ecosystem can be maintained is of crucial importance (Rockström et al. 2009; Cardinale et al. 2012).

This thesis provides evidence of how species richness promotes temporal stability in the productivity of plant communities (chapter 1 and chapter 3) and it elucidates the complex network of mechanisms behind it (chapter 1). I found that stability of more diverse communities is promoted by an increased temporal instability at the population level, that is, the biomasses of the different species fluctuate asynchronously and compensate each other, generating greater stability at the community level (chapter 1). These results were in line with previous findings (Flynn et al. 2008; Loreau and de Mazancourt 2008, 2013; Isbell et al. 2009) which recognized this phenomenon and referred to it as the "insurance effect of biodiversity" (Bai et al. 2004; Ives and Carpenter 2007).

Greater species richness was found to promote stability in productivity in a large number of experiments (for a summary see Hautier et al. 2014). This thesis shows that species richness promotes stability of community productivity both when species richness is artificially maintained (chapter 1) and when plant communities are allowed to reassemble naturally (chapter 3). This demonstrates that species richness can uphold greater stability in ecosystem productivity regardless of the origin of species richness. Moreover, my findings advocate the capability of biodiversity experiments to capture natural phenomena. Although

the reliability of biodiversity experiments to understand and predict natural processes has been questioned (Doak et al. 1998; Lepš 2004; Thomson et al. 2005), my work confirms once again that species richness, regardless of its origin, promotes productivity and stability of productivity over time.

Competition as a mechanism of species coexistence

The mechanisms of species coexistence have been largely debated and this dispute led to the identification of two opposite explanations (Cardinale et al. 2009): equalizing forces on one side, represented at the extreme by random events incorporated in neutral theory (Hubbell 2001; Bell 2001), and stabilizing forces on the other side, represented by the complementary use of resources via niche partitioning, embedded into the niche theory (Chesson 2000; Cardinale et al. 2009; Levine and Hille Ris Lambers 2009). Each chapter of this thesis shows that the mechanisms of niche complementarity and resource partitioning are largely but not exclusively responsible for species coexistence.

In chapter one I studied the drivers of temporal stability in community productivity. I show that measures related to biotic interactions (i.e. community structure and functional trait diversity) had a much stronger effect on community stability than measures related to abiotic influences (i.e. environmental fluctuations). Biotic drivers interacted both directly and indirectly – via promoting asynchronous species fluctuations – on community stability. In comparison with the measure of abiotic variation the measures of biotic interactions captured the role of intra- and interspecific species competition (Chesson 2000; Levine and Hille Ris Lambers 2009). Since I found that the role of abiotic drivers was much smaller than the role of biotic drivers, I suggest that in the Jena Experiment mechanisms of niche differentiation, more than mechanisms of species dominance, foster the stabilization of more diverse communities.

Additional support to this interpretation derives from the measure I used to quantify functional trait diversity. I measured functional trait diversity both as FD (Petchey 2003; Petchey and Gaston 2006) and as Community Weighted Mean of traits, CWM (e.g. Lavorel et al. 2008). These two methods support, respectively, a complementary use of resources through niche partitioning and a selection-effect mechanism where ecosystem processes are mainly determined by the dominant functional traits of the community (Roscher et al. 2012). I show that FD is a much stronger driver of community stability than CWM, thus corroborating the hypothesis that mechanisms of complementarity use of resources are largely responsible for community dynamics.

In chapter two, I predicted species coexistence on the basis of species-specific (growth rate and carrying capacity) and species-pair specific (interspecific competition coefficient) measures. In accordance with niche theory species-specific characteristics such as the differences in growth rates and carrying capacity can predict species coexistence and therefore community assembly (Levine and Hille Ris Lambers, 2009; Tanner et al. 2005). Predictions of species coexistence on the basis of the quantification of the competitive ability of each two-species pair and of species-specific characteristic consider only direct interspecific competition as a driver of species coexistence (Connolly et al. 2001; Connolly and Wayne 2005; Weigelt et al. 2007). Pairwise competition experiments and their analysis with Lotka-Volterra (LV) models have been extensively used to quantify the role of direct interspecific competition (Chesson 2000; Connolly et al. 2001; Connolly and Wayne 2005; Dormann and Roxburgh 2005; Weigelt et al. 2007; Engel and Weltzin 2008; de Mazancourt et al. 2013). However, the majority of the studies that applied LV models to real or simulated data (see above references) found only limited evidence for the role of direct interspecific competition in explaining species coexistence (but see Weigelt et al. 2007). Instead, in this study I found that direct interspecific competition is a relevant driver of species coexistence

during the establishment of the communities (chapter 2), thus suggesting how the role of direct interspecific competition might have been overlooked by previous studies.

Finally, in chapter 3, the strongest evidence for the role of niche partitioning in favoring species coexistence and therefore positive biodiversity effects on productivity, derives from the application of additive partitioning (Loreau and Hector 2001) to the communities in the Jena Experiment. Additive partitioning was developed to separate the contribution of selection-effect mechanisms, such as the effect of species dominance, from the contribution of complementarity among species, which relate to the presence of more niche-based mechanisms maintaining multi-species communities and their functioning (Loreau and Hector 2001). I show that complementarity effects in invaded areas (i.e. in communities where the weeding treatment was stopped and therefore natural reassembly processes could occur) were always positive and always larger than selection effects. Also, complementarity and selection effects in the core areas (i.e. areas where the weeding treatment was maintained) were much smaller than in the invasion areas, where both complementarity and selection effects ranged around zero. Therefore, these findings also suggest that through the optimization of the use of biotope space the species in the invasion areas of the Jena Experiment assemble in order to reduce the competition among co-occurring species in communities.

The relevance of the temporal scale

In natural environments populations and community dynamics are regulated by spatially and temporally heterogeneous resources (Paine and Levin 1981; Petraitis et al. 1989). Similarly, contrasting mechanisms such as complementary use of resources versus species dominance are likely to operate on different spatial and temporal scales (Cardinale et al. 2004; Hille Ris Lambers et al. 2012). However, the majority of biodiversity experiments whose aim was to further our understanding of natural communities lasted for a rather short period, typically

less than four years (Cardinale et al. 2007; Reich et al. 2012). As a consequence, the validity of biodiversity experiments has been questioned by some authors (Wardle et al. 2000; Cardinale et al. 2004). Additionally, the temporal scale is a relevant factor in biodiversity experiments *per se* because also under experimental conditions interactions between species develop and vary across time (Pacala and Tilman 2002; Van Ruijven and Berendse 2009). Thus, during the last decade long-term experiments have been advocated to study mechanisms underlying biodiversity effects (Symstad et al. 2003; Cardinale et al. 2004; Hooper et al. 2005; Zavaleta et al. 2010). The Jena Experiment with its now (2014) 12 years of continuous operation, constitutes an extraordinary tool to study those mechanisms, in particular temporal dynamics of species coexistence. Each chapter of this thesis emphasizes the importance of long-term data series to address ecological questions: in each chapter I show how the mechanisms that regulate biodiversity–ecosystem functioning relationships change or compensate each other across time.

In chapter one I found that the mechanisms promoting the stabilization of productivity of more diverse communities compensated each other across time. I showed that community structure, functional diversity and species richness were all similarly responsible for the temporal stability of the communities. These three drivers directly promoted community stability and promoted species asynchronous fluctuations, thus indirectly again promoted community stability. With structural equation modeling I showed that the effect of these drivers on community stability and on species asynchronous fluctuations changed over time and showed patterns of temporal compensation. The long-term dataset available from the Jena Experiment was thus an ineluctable prerequisite to the finding of these results.

In chapter two I found that LV-predictions of community performances were highly comparable to community performances observed in the Jena Experiment during the first years. From this high similarity between observed and predicted data I suggest that mechanisms of direct interspecific competition play a crucial role during the early phase of

community establishment to be later replaced by more complex indirect mechanisms and stochastic events. However, if the data collected from the Jena Experiment would not have included these later years, I would have not been able to detect other than direct interspecific competition measures defining species coexistence.

In the last chapter I could only consider a shorter time period. To analyze the mechanisms of community assembly I compared communities that were artificially maintained by weeding during the whole time of the experiment with communities where natural reassembly was allowed from 2009 onwards. Thus, I analyzed the mechanisms of species reassembly for a 4-years period. I found that species richness, species turnover and total biomass in the invasion areas (i.e. areas where natural reassembly was allowed) reached a plateau in year 2012. Since data were available only until year 2013 it is too early to assert that community compositions and community biomass fully stabilized across all communities after 3 years of the reassembly processes. Thus, to continue to measure community properties in the invasion areas would allow to test if and when the characteristics of the communities undergoing natural reassembly reach an equilibrium status. However, even though in chapter 3 I focused on a shorter time-span compared to the other chapters, mechanisms of species assembly trough the complementary use of resources became stronger over time.

Future development

The data I collected, combined with a number of other data available from the Jena Experiment, would allow furthering even more the understanding of the mechanism already discussed in this thesis. First of all, in this thesis I did not use any phylogenetic data. Phylogenetic data have been receiving an increasing attention from the scientific community (Webb et al. 2002; Cadotte et al. 2008; Cavender-Bares et al. 2009). For example, phylogeny has been shown to play a role in driving community assembly by shaping mechanisms of limiting similarity between closely related species and mechanisms of complementarity

between distant relatives (Allan et al. 2013). Thus, the use of phylogenetic data would allow deepening the understanding of the role of species relatedness on driving species coexistence.

Different studies have shown the role of plant–soil feedback mechanisms in defining increased complementarity in more species-rich communities (Klironomos et al. 2000; Wagg et al. 2011; Kulmatiski et al. 2012). These mechanisms were found and described also within the framework of the Jena Experiment (e.g. Eisenhauer 2012) but are not included in this thesis. Further development of this topic will come for the Ph.D. work of Sebastian Keller, University of Bern, who was my collaborator in the same project with focus of plant–pathogen and plant–herbivore interactions.

The mechanisms of biodiversity–ecosystem functioning can be investigated at different temporal and spatial scales. If this thesis has the advantage to investigate mechanisms of species coexistence on a long temporal scale (see previous section), it has the downside to focus mostly on a community-based approach. An analysis of species-specific dynamics (e.g. species demographic changes) would be of great help to further our understanding about the mechanisms regulating coexistence and therefore biodiversity–ecosystem functioning relationships, and some of these analyses are already possible with the data collected. In chapter 1 I focused on community responses to environmental changes. By following the procedure of de Mazancourt et al. (2013) it would be interesting to derive environmental variation indices from monoculture performances. This would allow us to quantify the speed at which the different species respond to perturbations (Loreau and de Mazancourt 2013).

The data collected for the analysis of chapter 2 offer a large number of alternative analyses. Here I will not discuss the possibility of improving the LV model, for example by implementing demographic and environmental stochasticity (e.g. de Mazancourt et al. 2013), but I will instead discuss approaches that may allow a more species-specific focus. Since both predicted and observed community properties are measured at the species level one

could analyze these data with different approaches such as the diallel mechanistic approach (e.g. Baruffol et al. 2014) that partitions the effect of particular species within the community to explain individual species effects or the competitive hierarchy approach (e.g. Tanner et al. 2005; Weigelt et al. 2007) that emphasizes the hierarchical relationships among species. Furthermore, the LV model could consider an additional measure of intraspecific competition in order to assess self-regulating dynamics and potential effects of plant–soil feedbacks on dominant species. However, due to the modular growth form of grassland species, it is questionable whether monoculture pots with two individuals can provide a good measure of intraspecific competition, especially given that the biomasses of monoculture pots with one and with two individuals were comparable (see chapter 2).

Finally, in chapter 3, a new approach would be to focus on the sequence of species arrivals in the community. If on one side it has been shown that relatively few species can promote community productivity, it has also been shown that different species can do so in different years and under different geographic and climatic scenarios (Isbell et al. 2011). Thus, species arrival, and therefore the history of community assembly, could be investigated (and partially it has been; see Roscher et al. 2014) in order to extend our understanding about the mechanisms of biodiversity–ecosystem functioning relationships (Fukami and Morin 2003; Isbell et al. 2011; Roscher et al. 2014).

Finally, a general recommendation is to increase the use of cover-based data in the study of mechanisms of biodiversity–ecosystem functioning. My thesis shows that cover-based data are an excellent tool to study biodiversity–ecosystem functioning relationships (chapter 3). In general, cover data measure realized diversity on a larger scale than what is usually measured in small biomass sample; cover data are therefore recommendable when estimating realized species richness and abundances (Rixen et al. 2008). Additionally, there is also a more applied aspect behind the use of plant cover data. In alpine grassland, it has been shown that plant cover itself (portion of the ground covered by plant species) is an

important ecosystem function in terms of prevention of erosion (Rixen et al. 2008). It might be of interest to investigate to which extent plant cover may help explain biodiversity–ecosystem functioning relationships involving others than productivity variables in grasslands. Additionally, since the use of cover data in this thesis was restricted to the analysis of the mechanisms of species coexistence (chapter 3), it would be recommendable to extend the use of cover data also to the other investigated mechanisms such as those of species coexistence and those regulating the increased stability of productivity of communities of higher species richness.

Conclusion

This thesis provides new insights into the mechanisms underpinning biodiversity–ecosystem functioning relationships. I showed how temporal stability of community productivity greatly depends on the maintenance of given community characteristics across time. Also, I showed how species competition influences mechanisms of increased temporal stability of more diverse communities, of species coexistence and of community assembly. How can these findings make a contribution to understand the consequences and processes that might mitigate the effect of biodiversity decline on the functioning of ecosystems? One answer, for example would be that conservation practices should shift from emphasizing emblematic species to the protection of species richness overall. Therefore, restoration efforts should be conceived in the light of the intricate nature of abiotic and biotic interactions that occur within ecosystems and their dynamics across different spatial-temporal scales.

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